ECOHYDROLOGICAL CONTROLS AND EFFECTS OF RHIZOME INTEGRATION ON THE PERFORMANCE OF *ARUNDO DONAX* IN A RIO GRANDE RIPARIAN ZONE

A Thesis

by

LI KUI

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2011

Major Subject: Rangeland Ecology & Management

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Approved by:

Co-Chairs of Committee,	Georgianne Moore
	Jason West
Committee Member,	Astrid Volder
Head of Department,	Steven Whisenant

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ABSTRACT

Ecohydrological Controls and Effects of Rhizome Integration on the Performance of *Arundo donax* in a Rio Grande Riparian Zone. (August 2011)

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Dr. Jason West

This study focused on an invasive riparian reed grass, *Arundo donax* L., a clonal plant of the family *Poaceae* that is widely distributed in North America. Water availability, including water taken up from the roots locally or transported from the neighboring ramets, may affect the performance of *A. donax* in riparian zones. The first objective was to find out how moisture gradients affected the performance of *A. donax* in riparian zones. I measured leaf photosynthetic rate, leaf $\delta^{13}C$ ratio, and plant growth-related parameters across two summer growing seasons at four transects perpendicular to the water course on the Rio Grande in South Texas. The second objective was to find out whether physiological integration existed in *A. donax* and how resource sharing, if any, affected plant growth. A rhizome severing experiment was conducted on five paired plots to compare growth-related parameters between plots with rhizomes severed and intact at 3, 7, and 11 weeks after treatment. Heavy water ($\delta\ ^2H$ ~1800‰) was applied on three 1-m^2 area over 3 successive days and rhizome samples were collected beyond the watering zone after 5, 24, and 48 hours of last watering.

At short-term scales, *A. donax* performance was adversely affected by both drought and inundated conditions; over longer time scales, plant performance decreased as water availability declined in general, but biomass and stem density were similar across moisture gradients. I also found evidence of physiological integration in *A. donax.* Water was transported through interconnected rhizomes at least 3.5 m; transport distances averaged 1.67 m. Rhizome severing stimulated higher ramet production initially but over longer periods produced shorter thinner stems with lower flood tolerance. However, after 11 weeks of re-growth, plot-level biomass was similar between plots with severed and intact rhizomes. These results suggest that performance of *A. donax* is affected by water availability in riparian zones; however, clonal plant plasticity, water use efficiency, and clonal integration ameliorate impacts of water stress on the performance of *A. donax*. Such traits enhance its resource use, which could potentially increase competitive ability rate of establishment, and extent of this invasive species in heterogeneous riparian environments.

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CHAPTER I

INTRODUCTION

Ecohydrology is an interdisciplinary subject that involves the studies of both ecology and hydrology (Baird and Wilby 1999, Crawford 2000). In semiarid regions, where water is a primary driver of ecosystem processes, ecohydrology is concerned with two major questions: how land use or change of vegetation cover affects hydrological processes (Wilcox et al. 2005, Huang et al. 2006, Wilcox et al. 2006, Mark and Dickinson 2008, Wilcox et al. 2008, Wilcox and Huang 2010) and how hydrological processes affect the performance of single species or plant communities (Osterkamp and Hupp 1984, Hupp and Osterkamp 1985, Stromberg and Patten 1990, Smith et al. 1998, Merritt and Wohl 2002, Orfanus and Eitzinger 2010). My study focused on the later question and specifically how water availability affects plant performance in riparian zones.

Riparian ecosystems are among the most diverse terrestrial communities (Naiman and Décamps 1997). The major biotic component of the riparian ecosystem is vegetation, which tends to grow parallel to streams or rivers (Patten 1998). Closer to the river, mesophyte plants are commonly dominant, while xerophytes tend to grow further away as moisture decreases (Hupp 1982). In particular in semiarid regions, *Populus fremontii*, *Salix gooddingii (Snyder et al. 1998)*, *Tamarix ramosissima* (Busch et al. 1992, Smith et al. 1998), and *Prosopis glandulosa* (Weltz and Blackburn 1995) are the major riparian woody species. Loss or reduction in cover of these species can be an

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This thesis follows the style of Ecology.

indicator of soil moisture or groundwater decline (Stromberg et al. 1996). The diversity and distribution of plants in riparian zones are likely related to environmental gradients such as: hydrological conditions (Osterkamp and Hupp 1984, Hupp and Osterkamp 1985, Allendiaz 1991, Stromberg et al. 1996, Gomes and Asaeda 2009), substrate sediment size (Ware and Penfound 1949, Frye and Quinn 1979), and flood event size and frequency (Grime 1974, Stromberg and Patten 1990). The primary environmental factors that determine species composition may change seasonally and are likely to interact. Data on how such factors regulate plant distribution and growth are crucial in developing management plans aimed at maintaining high species diversity while reducing the amount of invasive plants.

Plants may rely on different water sources, depending on species, age, and rooting depth (Stromberg and Patten 1990, Dawson and Ehleringer 1991). There are potentially three major water sources in most riparian zones: groundwater, river water, and precipitation. Phreatophytes such as *Populus fremontii* (Dawson and Ehleringer 1991) and *Salix gooddingii* (Horton et al. 2001) rely heavily on groundwater supplied by the alluvial aquifer. Herbaceous plants can also access groundwater, such as described in Dwire's (2004) research on sedge species. Access to river water via the alluvial aquifer can also affect distribution of riparian species. Stromberg and Patten (1990) found that mature riparian species composition in the south-western U.S. was primarily determined by distance from the river as highly flood tolerant plants were located closer to the water course. Some deep-rooting plants can switch their water sources between groundwater and surface soil moisture in response to changing precipitation patterns and water

availability, such as *Prosopis velutina* (Snyder et al. 1998). In my thesis, groundwater and surface soil moisture are considered to be the two major water sources for regulating the growth of plants.

Many riparian habitats have been degraded by both direct and indirect influences of human activities. Land use change and alteration of components of the hydrologic cycle are known to have a strong impact on the abundance, structure, composition, productivity, and functional integrity of riparian zones (Patten 1998). For example, dams reduce flood frequency, magnitude, and timing (Stromberg and Patten 1990, Stromberg et al. 1993, Busch and Smith 1995, Stromberg et al. 1996), which favors the establishment and proliferation of non-native vegetation. Declining water tables and streamflow can reduce the vigor of riparian vegetation and ultimately can cause its death and prevent re-establishment. Such is the case in the southwestern US that native *Populus fremontii* and *Salix gooddingii* are gradually replaced by *Tamarix* (Stromberg et al. 2007). Riparian zones become exceedingly vulnerable to invasion by exotic plants in part because invasive species are more highly competitive, flood and salinity tolerant, widely adapted to extreme conditions, and favor altered hydrological conditions (Boose and Holt 1999, Hood and Naiman 2000, Culliney 2005, Decruyenaere and Holt 2005, Gilbert and Lechowicz 2005).

Exotic plants are a key component of global environmental change. Because of expanding human activity, more plants have been introduced, some of which grow aggressively and out-compete the native vegetation (Brock et al. 1997). There are increasing concerns about the expansion of invasive species, which not only reduce

biodiversity (Dietz et al. 2002, Jakobs et al. 2004, Gilbert and Lechowicz 2005) , but also influence water resources (Stromberg et al. 2007) and soil properties locally (Blank et al. 2002, Ehrenfeld 2003, DeCant 2008). Broadly, successful invasion depends on attributes of the invasive species (Jia et al. 2009, Pysek et al. 2009) and the surrounding environmental condition (Pan et al. 2006). Narrowing down to an individual invasive species at a local scale, successful invasion is often controlled by some specific environmental factor, such as soil water or nitrogen availability (Dawson and Holland 1999, Loo et al. 2009).

Among groups of invasive species, clonal plants are unique. Clonal growth is asexual production of physiologically complete plants (De Kroon and Schiving 1990). This group of plants, commonly perennial herbs as well as grass and grass-like species (Pysek et al. 2009), reproduces from rhizomes or stolons (Caraco and Kelly 1991, Lambers et al. 1998) . One individual clonal offshoot is referred to as a ramet, which can independently regenerate offspring. In general, clonal plants can transport water, nutrients, and other resources through the interconnected rhizomes, which can raise the survival rate and support the growth of ramets in harsher environments (Xiao et al. 2010). Clonal plants can exhibit high plasticity by altering rhizome length (Halassy et al. 2005), branching intensity (De Kroon et al. 1994), and biomass allocation (Asaeda et al. 2009) to adapt to different stressful environments. Clonal plants can propagate in resource limited places, such as sandy floodplain deposited following floods, and shares resources stored in the rootstock through interconnected rhizomes (De Kroon and Schiving 1990, Hood and Naiman 2000). This can significantly benefit the growth and

spread of the plants in heterogeneous riparian conditions; whereas, non-clonal riparian plants tend to be restricted to very wet and nutrient-abundant sites (Prach and Pysek 1994, Maurer and Zedler 2002, Xiao et al. 2011).

This study focuses on an invasive riparian reed grass, *Arundo donax* L., a clonal plant of the family *Poaceae* that is widely distributed in North America (Bell 1997, Dudley 2000). *A. donax* is also called giant reed or carrizo cane, one of the top 100 most severe invasive species (Bell 1997). It is believed to be native to eastern Asia (Polunin and Huxley 1978), but has been cultivated for thousand years in other parts of world: southern Europe, North Africa, Middle East, and Mediterranean basin (Perdue 1958, Bell 1997). It was intentionally brought to North America by colonists for use in musical instruments, thatching, basket weaving, and erosion control (Perdue 1958, Polunin and Huxley 1978, Milton 2004). After naturalizing in North American in the 1800's, it expanded into the lower half of the United States from California to Virginia (TNC 1996, Bell 1997, Everitt et al. 2004).

Arundo donax is a typical clone species, which ramets are connected by belowground rhizomes. It does not reproduce from seeds in North America (Decruyenaere and Holt 2001). Instead, it propagates vegetatively, expanding from horizontal root stocks, rhizomes, or growing from stem fragments (vanGroenendael et al. 1996, Dudley 2000, Spencer and Ksander 2006). *Arundo donax* places ramets towards resource-abundant habitats, where the individual ramets can gain local resources (Halassy et al. 2005). It is possible that some ramets of *A. donax* remain integrated physically and physiologically for resource sharing, which might benefit the

establishment and expansion of *A. donax* in riparian zones. However, little research is focused on *A. donax* with regards to resource sharing.

Arundo donax is a typical hydrophyte and prefers to grow in wet areas (Spencer et al. 2005, Quinn and Holt 2008), such as along rivers, streams, and drainage ditches (Perdue 1958, Bell 1997). *Arundo donax* has formed extensive stands in the lower Rio Grande basin of southern Texas. Because it grows along the waterway, flood events can break up ramets of *A. donax* and wash fragments downstream, where it can clog waterways and irrigation canals and destroy bridges (Bell 1997). Furthermore, a fast-growing stand of *A. donax* may reduce river flows and may contribute to the water level decline. In order to support its incredible growth rate (5 cm per day) and vast amount of biomass (Perdue 1958, Angelini et al. 2005, Quinn and Holt 2008), it is estimated to consume an average of 9.1 mm of water per square meter of standing crop daily (Watts 2009), which is higher than other riparian herbaceous species, such as *Carex.* If the roots cannot reach enough water and resource sharing does not exist within the patches, performance of *A. donax* might be constrained to some extent.

Arundo donax is a very competitive plant that forms extensive stands in riparian zones. In some habitats, it is much more biologically productive than other plants (Boose and Holt 1999, Khudamrongsawat et al. 2004, Decruyenaere and Holt 2005, Quinn et al. 2007). Unfortunately, these large amounts of biomass cannot provide food for native species of wildlife because they contains noxious chemicals (Miles et al. 1993, Guthrie 2007). Because it gradually takes over other vegetation in the riparian zones, the wildlife that originally relied on other plant species would be imperiled, which further enhances

the decline of riparian biodiversity. Dense stems growing along the river bank can also accumulate sediment, which may speed up the processes of channelization and river migration (Hupp and Osterkamp 1996, Bell 1997). In addition, because the plant material is also highly flammable, *A. donax* is reported as a fire hazard in the semiarid regions (Boose and Holt 1999). Therefore, establishment and expansion of *A. donax* are most likely to degrade the riparian zones and adversely affect the local biodiversity.

The lower Rio Grande of Texas is situated within a semi-arid region. It is an international boundary river, in which competition for water has caused social and environmental conflicts between the U.S. and Mexico (Sagaz 2010). Historically, the water of the Rio Grande flowed into the Gulf of Mexico (Drinkard 2009). However, in recent years intermittent and low flows have occurred in the lower sections of the river, mostly due to over pumping for irrigation and municipal water demand and drought conditions (Small et al. 2009). In part, because of altered hydrological conditions, native riparian species, such as *Populus* and *Salix*, have declined (Small et al. 2009) in favor of invasive species, such as *Arundo donax* (Yang et al. 2009), *Tamarix chinensis* (Owens and Moore 2007), and *Elaeagnus angustifolia* (DeCant 2008). Studies focused on plant invasion along the Rio Grande may be able to improve our understanding of the effects of plant invasion on the function of local vegetation communities and guide future research.

Despite considerable progress toward understanding the ecology and evolution of *A. donax* achieved in the last decades, our knowledge is still based on relatively few case studies or greenhouse studies, which almost exclusively deal with its impacts in

California. There are some common attributes between Texas and California and some of the research conclusions might also apply in Texas. However, understanding plant performance associated with its unique environmental factors in riparian zones in southern Texas is important for local invasive species management and water conservation.

My thesis focuses on the ecohydrological controls on the performance of *Arundo donax* in a riparian zone of the Rio Grande. I use both observational and experimental studies to evaluate the relationship between water availability and plant performance. I proposed here four hypotheses. First, the performance of *A. donax* (photosynthesis, biomass, stem height, and density) is positively related to water availability (ground water, moisture in top soil). To test this hypothesis, I conducted an ecological survey on natural-populated *Arundo donax* stands growing along riparian zones of the Rio Grande. For the second hypothesis, I hypothesized that water availability is influenced by floodplain geomorphological factor such as elevation and soil texture. To test this hypothesis, relationships among soil moisture, relative elevation, soil texture, and distance from the river were analyzed. Thirdly, I hypothesized that *Arundo donax* shares resources (i.e., water) through interconnected rhizomes. To test this hypothesis, I applied deuterium enriched water on plant patches and traced the movement of the enriched signal beyond the watering zones. The fourth hypothesis was that clonal integration of *A. donax* enhances clonal reproduction and performance of *Arundo donax*. To test this hypothesis, I carried out a rhizome severing experiment after which the recruitment and morphology of plants between severed and non-severed treatments were compared.

Hypotheses one and two are addressed in Chapter II, while hypotheses three and four are addressed in Chapter III. The final chapter of the thesis presents conclusions and discusses the implications of my findings for *A. donax* management.

CHAPTER II

ECOHYDROLOGICAL CONTROLS ON THE PERFORMANCE OF *ARUNDO DONAX*

INTRODUCTION

In semi-arid regions, such as the lower Rio Grande River, water is the primary factor that affects vegetation vigor (Gordon et al. 1999) and distribution in riparian zones (Osterkamp and Hupp 1984, Hupp and Osterkamp 1985, Allendiaz 1991, Stromberg et al. 1996, Midwood et al. 1998, Gomes and Asaeda 2009). Environmental gradients, in particular water gradients, commonly occur in riparian zones due to heterogeneous moisture conditions from river to the upland, including elevation change. Riparian plants can acquire water from soil moisture (Busch and Smith 1995), groundwater (Frye and Quinn 1979), or both (Snyder et al. 1998). Additionally, the duration of flood inundation or saturation can also play a strong role in semiarid rivers, due to differential species tolerances for soil saturation (Robertson et al. 1978, Hupp and Osterkamp 1985, Auble et al. 1994, Bell 1997, Rossa et al. 1998, Kirkham 2005). Plant communities subjected to water gradients tend to develop distinct patterns in species composition (Hupp 1982), plant distribution (Osterkamp and Hupp 1984, Hupp and Osterkamp 1985, Allendiaz 1991, Stromberg et al. 1996, Gomes and Asaeda 2009), species richness (Frye and Quinn 1979, Horton et al. 2001), and plant biomass (Heathcote et al. 1987, Williams and Black 1993, Riis et al. 2001, Dwire et al. 2004). In semiarid riparian zones, most research has focused on woody species such as *Populus fremontii* and *Salix gooddingii*

in terms of plant distribution pattern and community composition (Busch and Smith 1995, Stromberg et al. 2007). Limited data are available on spatial differences in hydrologic and edaphic gradients along the riparian zone and how these related to performance of herbaceous species (Castelli et al. 2000).

Riparian gradients in nitrogen might also lead to distinct vegetation patterns (Evans 1989, Zheng and Shangguan 2006, Gomes and Asaeda 2009, Griffith et al. 2009). If the river has excess nutrients from anthropogenic sources (Spink et al. 1998), such as is the case with the Rio Grande (Drinkard 2009), then it is possible that plants growing closer to the river might not be nitrogen-limited while those farther away might be.

Resource gradients may impact plant performance in the short term by reducing stomatal conductance, which impacts rates of photosynthesis (Svejcar and Trent 1995, Lambers et al. 1998). If stomatal conductance is reduced for longer periods, water use efficiency changes would be reflected in leaf carbon stable isotope ratios (Farquhar and Richards 1984, Martin and Thorstenson 1988, Midwood et al. 1998, Robinson et al. 2000, Dawson et al. 2002). Leaf carbon stable isotope ratio is a time-integrated response to water availability over a set time period such as the life span of a leaf, an entire growing season, or a year (Farquhar et al. 1982, Farquhar and Richards 1984, Ehleringer 1990, Ehleringer and Cerling 1995, Osorio et al. 1998, Dawson et al. 2002). Over the course of a growing season, reductions in photosynthesis eventually lead to slower growth rates, which are reflected in biomass and height. Understanding water-plant relationships in the short-term may offer insights into how sensitive the plants may be in

response to changes in abiotic conditions (Campbell and Grime 1992, Dudley 1996, Thevs et al. 2007, Asaeda et al. 2009).

With regards to longer-term plant performance in response to environmental gradients, morphological plasticity has been shown in some clonal plants, which might give them an advantage in spatially heterogeneous riparian environments (Lynch 1984, Bierzychudek 1985, Sutherland and Stillman 1988). Common clonal plants in riparian zones are *Phragmites australis* (Amsberry et al. 2000, Lenssen et al. 2000), *Phragmites japonica* (Asaeda et al. 2009), *Alternanthera philoxeroides* (Jia et al. 2009), *Glyceria maxima* (Loo et al. 2009), and *Eragrostis curvula* (Gomes and Asaeda 2009). These plants typically form monocultures that reduce riparian biodiversity (Dwire et al. 2004). Morphological plasticity in clonal plants in response to environmental heterogeneity has been shown to be very important for clonal plant functioning (Cook 1985). We haven't yet studied plasticity in enough species or under dynamic conditions (wet to dry gradients) to determine necessary generalizing principles (De Kroon et al. 1994). The research presented in this thesis contributes to a better understanding of morphological plasticity of clonal plants along environmental gradients.

This study focuses on an invasive riparian reed grass, *Arundo donax* L., a clonal plant of the family *Poaceae* that is widely distributed in North America (TNC 1996, Bell 1997, Dudley 2000, Decruyenaere and Holt 2001). *Arundo donax* tends to grow in riparian habitats, floodplains, ditches, and irrigation canals, (Quinn and Holt 2008). Extensive stands of *A. donax* grow on the Rio Grande riparian zone in Texas at a density of about 4.5 ha/km (Yang et al. 2009).

There are two major reasons for selecting *Arundo donax* to study plant-water relationship along riparian zones. First, it grows extensively along the lower Rio Grande riparian zones where moisture and nitrogen gradients exist. It is not known how the performance of *A. donax* within these extensive stands is limited by gradients in moisture (surface soil moisture and access of groundwater), nitrogen, and soil textures. Second, since *A. donax* typically invades semi-arid riparian ecosystems, it may exhibit excess water consumption (Bell 1997). Because of enormous water demand, moisture gradients may significantly affect the performance of *A. donax*. To date, most studies on *A. donax* were conducted in the greenhouse or in the field using plant cuttings (exception see (Spencer, 2005)). Those manipulative experiments can help to directly understand single factors that limit the performance of *A. donax*. Field experiments can further expand our knowledge about integrative environmental gradients and how those affect plant performance.

I conducted an ecological survey on naturally-populated *Arundo donax* stands growing along the riparian zones of the Rio Grande. There were two hypotheses. The first hypothesis was the performance of *A. donax* was positively related to water availability. In the observational studies, leaf photosynthetic rate and leaf $\delta^{13}C$ ratio represented short-term and time-integrated response to water availability, respectively. Plant density, plant height, and aboveground biomass represented plant response to water over longer term scales (a season or more). The second hypothesis was that water availability was influenced by floodplain geomorphology because of elevation and soil texture.

MATERIALS AND METHODS

Study Site and Climate

Research sites were located on the active floodplain of the lower Rio Grande between Del Rio and Eagle Pass in southern Texas (29°14'44"N, 100°47'38"W to 29° 9'45"N, 100°45'43"W) in extensive stands of *A. donax* with sparse individuals of honey mesquite (*Prosopis glandulosa* Torr.) in some locations. Rarely (<1% cover) were assemblages of herbs grown in the *A. donax* patch in which most common families were *Ranunculaceae*, *Verbenaceae*, *Malvaceae*, and *Lamiaceae*.

The mean annual precipitation is 477 mm $year^{-1}$ and monthly average temperatures ranges from 10 °C in winter to 27 °C in summer. Two-thirds of the annual precipitation (~198 mm) occurs in the late summer and early fall (Drinkard 2006). In summer 2009, the area experienced a drought that persisted for several months while average monthly temperature was above 30-year climate normal (1980-2010) from January to August. Total precipitation for May to August in 2009 was 96 mm, less than half of normal precipitation amount for that period over the past 30 years (Table 2.1). By the end of summer of 2009, some of *A. donax* located on the upland had died back (Pers. Obs.). 2010 was a relatively wet year compared with 2009. Total precipitation from May to August 2010 was 417 mm, twice the normal rainfall amount for this period. In May 2010, the precipitation was 265 mm, which was 5 times higher than the climate normal for that month (Table 2.1). At the end of May, this area experienced a small flood with only partial inundation of one transect (transect 4) for 2 days. During a large flood event in 2010, all sites were partially to fully inundated for the period of July 7th to July 15th.

After the flood, the river continued to flow at higher than normal levels until the end of August.

Table 2.1. Precipitation and temperature data from National Weather Service (NOAA 2010a, b). 2009 was dry and hot, while 2010 was wet and relatively cool.

	Precipitation (mm)				Temperature (°C)			
	May	June	July	August	May	June	July	August
2009	12.4	77.7	4.3	1.52	27.0	30.7	32.2	31.7
2010	265	18.0	119.9	14.5	25.2	29.4	28.5	31.1
Climate normal	58.6	59.4	51.3	54.9	25.4	27.5	29.6	29.1

Four permanent transects were constructed perpendicular to the water course along the Rio Grande. Transects 1 and 4 were located in convex meanders and transects 2 and 3 were located in concave meanders. We chose convex and concave reaches of the river to allow assessments of their potential role in controlling the environmental conditions experienced by *A. donax*. Transect 1 was bound by a cliff approximately 120 m away from the river. Transect 4 had steep slopes starting uphill from the edge of *A. donax* patch, while transects 2 and 3 located in the middle of floodplain. The lengths of transects 1-4 depended on the width of continuous *A. donax* distribution, from the edge of the river to the other ends of transect, 105, 105, 125, and 69 m, respectively. Distance between the northern-most transect (transect 1) and southern-most transect (transect 4) was approximately 10 km, and distances ranged between 1 km to 5 km between each

transect. Fire had burned the *A. donax* stands in the recent past as evidenced by charred standing dead biomass, yet the stands had recovered robustly.

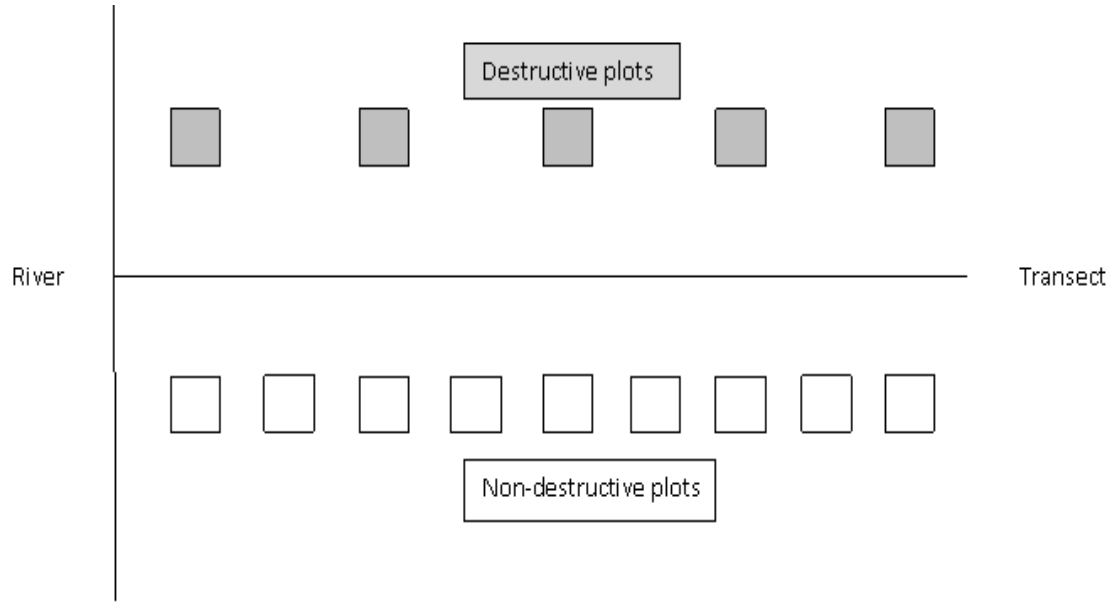

Figure 2.1. Plot layout for each transect. In total, there were 9 plots on one side reserved for non destructive measurements (P1-P9 from river to upland); whereas, there were 5 plots on the opposite side for destructive measurements (P1, P3, P5, P7, and P9 from river to upland).

Within each transect, access to study plots was obtained via a cleared 2-m-wide path extending the entire length (Figure 2.1). Nine plots served for non-destructive measurements such as photosynthesis and soil moisture, and were placed at equal distances along each transect, 2 m from the path. On the opposite side of each transect, five 1-m^2 plots were used for destructive measurements, such as soil coring and plant harvest. 4-m-wide horse trails that intersected our transects were found on two of the sites approximately 15 m away from the river, but plots were located away from these

trails. All of our sites were located in the quarantine areas used to contain the fever tick (Pound et al. 2010).

Table 2.2. Summary table for measurements taken in 2009 and 2010.

Measurement	2009	2010
Photosynthesis	1 set	3 sets
Aboveground biomass	1 set	1 set
Belowground biomass	1 set	none
Stem density	1 set	1 set
Leaf carbon isotope	1 set	3 sets
Leaf Nitrogen content	1 set	3 sets
Depth to the ground water	Estimated based on gage data in 2010	3 sets
Soil moisture	1 set	3 sets
Relative elevation	Same as 2010	1 set
Soil texture	1 set	Same as 2009
Distance from the river	Same as 2010	1 set

Leaf Photosynthetic Rate

I measured leaf photosynthetic rate using a LI-COR 6400 (LI-COR, Lincoln, NE, USA). Measurements were taken between 8 a.m. and 1 p.m., when plants were most actively photosynthesizing (Watts 2009). The second fully-expanded leaf from the tallest stem in each plot was used for measurement. The chamber was controlled at a constant level of light set to 1600 μmol m^{-2} s^{-1} using an internal LED light source to obtain the photosynthesis rate under saturated light conditions (Watts 2009). Air flow rate was set

to 400 μmol $s^{-1}$and CO_2 levels were set to 385 ppm. Humidity and temperature inside the measurement chamber were set to close to ambient conditions before measuring each leaf.

There were four full sets of leaf gas exchange measurement over two years (Table 2.2). In 2009, since the measurements had to be done after each transect was built, data were collected on different days: July 20th, Aug 5th, Aug 19th and 20th, on transect 4, 3, 1 and 2, respectively. The other three sets of measurement were taken on all transects in 2010 at intervals of 3-4 weeks. Those dates were June 7th-8th, July 20th-26th, and Aug 12th-13th. Measurements on June 7th-8th and Aug 12th-13th were taken approximately 2-3 weeks after flooding. The set in July 2010 was taken in each transects three times in a row, separated two days apart after the water began to subside and all transects were still partly inundated. July 2010 was the only case where a "set" was represented by averaging repeated measurements taken in close sequence.

Stem Density, Stem Height and Aboveground Biomass

In 2009, *Arundo donax* was harvested from five 1-m^2 destructive plots on 13th and 14th August (Table 2.2). Here, all stems were cut at ground level. The stem heights were measured from the base of plant to the top node of stem. In addition, the number of live stems per plot was counted for stem density. Live biomass was sorted from aboveground materials, and then weighed after 60 °C oven-drying to a constant weight. On Aug 16th-19th 2010, to avoid cutting effects from previous year and also increase the samples size, aboveground biomass was harvested in the plots right between each of two destructive plots, plus one extra plot right on the river bank. Plant height and density were

determined in the field. Aboveground biomass was estimated based on the relationship between total plot stem height and dry weight generated from 2009 (biomass = - 250 + 40.5 × height, $P < 0.05$, $R^2 = 0.90$).

Belowground Biomass

Belowground biomass was collected on August 13th-14th 2009 (Table 2.2). In the same plots as aboveground harvest, soil cores were collected from top 1-m of the soil profile at 20 cm intervals using a 5.4-cm diameter soil sampler. Belowground material was first run through a 2-mm sieve. Rocks and other foreign material were removed and the remaining coarse root material was washed and oven-dried at 60°C to a constant weight. Coarse root mass was separated into rhizomes and roots. Additional fine roots < 2 mm were separated by flotation in a saturated NaCl solution (density = 1.2 g/cm) for 2 hours. Floated material was collected using a vacuum filtration set. They consisted primarily of live and dead roots, as well as a few fragmental rhizomes and fragments of aboveground litter, but no attempt was made to separate these materials. Since non-root material was only up to 2% (visually estimated), it was not likely to cause big errors. The material collected from vacuum oven-dried at 60°C to a constant weight and added to the root material > 2 mm. In the end, rhizomes and roots were weighed separately.

Distance and Relative Elevation

Along each transect, the distance from the river and elevation of each plot was measured using a Total Station (Leica Geosystems, South Pasadena, CA). In 2010, wells were installed in each transect approximately 5-m away from the river, close to plot 1 of each transect. Water levels in each well were recorded concurrent with photosynthesis

measurements. River stage data were collected from the International Boundary and Water Commission website (www.ibwc.gov).

Relative elevation is the distance from water surface to ground surface of each plot. Based on the preliminary data (data not shown), time-integrated groundwater level was generally equal to the river level across all four transects. River stage data showed that Jun14th and Jun 21st 2010 stayed around 0.6 m (± 0.1 m), which indicated no flood event was happening. Well water levels measurements from these two days were averaged and then used to present the relative elevation of well, with 0 set at water surface. Then, relative elevations of plots were calculated based on the relative elevation of the well and the vertical distance between plots and well. Therefore, relative elevation can represent long-term proximal plot position above the water table. Lower relative elevation indicates easier access to the groundwater.

Additionally, depth to the groundwater of each plot on a given day (± 1 hour from time of photosynthesis measurement) was calculated using similar procedure as relative elevation but ground surface of each plot was set as zero instead of well water. Therefore, depth to the groundwater was negative number or zero for all the plots. In addition, depth to the groundwater for all plots in 2009 was estimated because lack of well data as follows. River stages of 2009 were 0.55 m on the date I measured photosynthesis in T3 and 0.74 m on the date I measured photosynthesis in other transects (± 0.01 m). Well water level data from Jun 25th and Jun 7th of 2010 were used on the depth to the groundwater calculation, respectively, because the stage data were the same (± 0.05 m).

Soil Moisture

The device used for volumetric water content measurements (%) was a capacitance probe Diviner 2000 (Sentek Pty Ltd, Stepney, South Australia). Five 2-m diviner access tubes were installed adjacent to plots reserved for non-destructive measurement along each transects in July 2009. Only one set of measurements were taken in 2009, Aug 19th-20th, after installing access tubes (Table 2.2). In 2010, measurements were repeated at 1-2 weeks intervals from June to August in 2010 (no measurement during flooding period between Jul 7th to Jul 15th). Soil moisture was measured at 10-cm depth increments from 0-100 cm depth.

Soil Texture

Soil texture was determined for soils sampled from belowground biomass harvest in August 2009 (described above) by using a hydrometer method (Bouyoucos 1962) (Table 2.2). After oven drying at 110°C, 50 g of sieved soil from each plot and 20-cm depth increment was soaked in 50 ml of dispersal agent ($NaSO_4$ solution) for 12 hours. The solution was transferred into a metal mixer cup followed by 5-minutes of mixing using a soil dispersion mixer (Colonial Scientific Inc, Richmond, VA). The solution was then transferred into a 1-L jar and filled with deionized water. After stirring solution 20 times using a stirring rod, 20-second and 2-hour readings from hydrometer were recorded to determine sand and clay content, respectively.

Leaf and Soil Nitrogen Concentration, Leaf Carbon Stable Isotope Ratio

Nitrogen concentration and ^{13}C of leaves used for photosynthesis measurement and soil from the top 20-cm was determined for each of the 9 plots plus one additional

plot on the edge of the river. Leaves and soil were dried at 60 ^{0}C to a constant weight. Leaves were ground using a freezer mill (SPEX, Metuchen, NJ) and a ball mill (Retsch, Newtown, PA) and soils were ground using a roller grinder (Watts 2009). Before grinding, soil samples were sieved through a 2-mm sieve in order to remove rocks, litter, and large root fragments. Subsamples of leaves (1.5 mg ± 10%) and soils (30 mg ± 10%) were run on a Isotope Ratio Mass Spectrometer coupled to an Elemental Analyzer (EA-IRMS; Thermo Fisher Scientific, Waltham, MA).

The leaf carbon stable isotope ratio was expressed as a delta notation ($\delta^{13}C$) in parts per thousand (‰) relative to the internationally reference standard, Pee Dee Belemnite (PDB) (Dawson et al. 2002):

$$\delta^{13}C\,(‰) = (R_{sample} / R_{standard} - 1) \times 1000\ ‰$$

where R_{sample} and $R_{standard}$ presented $^{13}C/^{12}C$ ratio in the sample and standard, respectively.

Statistical Analysis

All data were analyzed in JMP v.8 (SAS Institute, Cary, North Carolina). The F-statistic in all statistical analysis was considered significant at $\alpha = 0.05$. The data were tested for normality before ANOVA test and analyses were framed in the sequence of my two hypotheses.

For the first hypothesis, ANOVA followed by Tukey-Kramer HSD test was run for testing the difference among four sets of measurements (August 2009, June, July, August 2010: 200908, and 201006, 201007, 201008). Photosynthesis, soil moisture, relative elevation, leaf nitrogen content, and leaf $\delta^{13}C$ ratio were response variables. In

addition, photosynthesis and leaf $\delta^{13}C$ ratio data from 2010 were tested for differences among soil moisture groups (0-25, 25-30, 30-35, 35-40, and 40-55 %) to determine whether they varied along a soil moisture gradient. To understand the inundated condition in soil profile, I calculated percentage of saturated soil profile by using number of saturated soil layers divided by total (10 layers) for each plot, based on the assumption that soil was saturated if soil moisture reached 40 % for sandy loam soil (Kirkham 2005).

For the plant structure variables, linear regression was used to test relationships between long-term plant responses (aboveground biomass, belowground biomass, stem height, and stem density) and corresponding environmental factors (relative elevation and distance from the river).

For the second hypothesis, linear regression was used to test relationships among environmental factors (relative elevation, soil texture, soil moisture, soil nitrogen concentration, and distance from the river) to determine if soil moisture was related to floodplain geomorphology, which can manifest as gradients in elevation, soil texture, and soil nitrogen concentration that vary with relative elevation and distance from the river.

RESULTS

Across four sets of measurements, variation in photosynthesis was related to soil moisture (Table 2.3). Photosynthetic rates in August 2010 were significantly higher than those measured in August 2009 and July 2010. However, as soil moisture increased to 36 % in July 2010, photosynthetic rates were as low as they were in August 2009. In

order to understand how photosynthesis responds to high soil water conditions, I focused on 2010 only (Table 2.3), when photosynthesis measurements were taken during flooding and approximately 2-3 weeks after flooding. There was no statistically significant effect of soil water content on photosynthesis (Table 2.3).

Associated with soil moisture trend, depth to the groundwater was lowest in Aug 2009 and highest in Jul 2010 (Table 2.3). Additionally, plant available nitrogen also had similar trend as photosynthesis (Table 2.3). Lower photosynthesis exhibited in 200908 and 201007 were associated with lower leaf N.

Leaf samples from Aug 2009 had the highest leaf $\delta^{13}C$ ratio, which was 2.14 ‰ enriched compared to the mean of 2010. August 2009 also had the lowest soil moisture and deepest groundwater table of all measurement dates (Table 2.3). During 2010, plants were mostly under well-water conditions and exhibited less water use efficiency compared to 2009. In 2010, plants growing in the wettest soil (40-55%) had the highest $\delta^{13}C$ by 4.4% compared to the plants growing in the driest soil condition (0-25%) (Table 2.3).

Table 2.3. ANOVA table for means of different groups. Asterisk stands for significant difference at least between two groups. 200908, 201006, 201007, 201008 were time of four measurement periods. 0-25, 25-30, 30-35, 35-40, and 40-55% were the ranges of soil moisture corresponding to the measurements of photosynthesis and leaf carbon stable isotope ratio. The letters represent the significant difference between groups.

Response Variables	Groups	Means (±1SE)	F Ratio	Prob > F
Photosynthesis	200908	11.98(±0.65)[b]	3.97	0.0095*
	201006	12.65(±1.39)[ab]		
	201007	10.95(±0.90)[b]		
	201008	16.09(±1.35)[a]		
	0-25	13.88(±2.39)[a]	1.57	0.1953
	25-30	16.12(±3.11)[a]		
	30-35	15.60(±2.32)[a]		
	35-40	13.41(±2.67)[a]		
	40-55	9.00 (±1.75)[a]		
Soil moisture	200908	21.81(±2.21)[a]	6.55	0.0006*
	201006	29.67(±1.73)[ab]		
	201007	36.39(±2.58)[b]		
	201008	30.00(±2.42)[ab]		
Percentage of saturated soil layer	200908	9.38(±4.13)[a]	4.63	0.0052*
	201006	20.55(±5.60)[ab]		
	201007	45.11(±8.88)[b]		
	201008	24.74(±7.11)[ab]		
Depth to ground water	200908	-2.64(±0.17)[c]	7.07	0.0002*
	201006	-2.47(±0.18)[bc]		
	201007	-1.65(±0.19)[a]		
	201008	-1.81(±0.19)[ab]		
Leaf nitrogen concentration	200908	1.90(±0.06)[c]	10.69	<0.0001*
	201006	2.45(±0.08)[a]		
	201007	2.09(±0.08)[bc]		
	201008	2.23(±0.07)[ab]		
Leaf carbon stable isotope ratio	200908	-25.69(±0.22)[a]	40.97	<0.0001*
	201006	-28.06(±0.11)[b]		
	201007	-27.76(±0.14)[b]		
	201008	-27.62(±0.18)[b]		
	0-25	-28.46(±0.37)[b]	3.39	0.0155*
	25-30	-28.11(±0.30)[ab]		
	30-35	-27.65(±0.19)[ab]		
	35-40	-28.01(±0.20)[ab]		
	40-55	-27.25(±0.23)[a]		

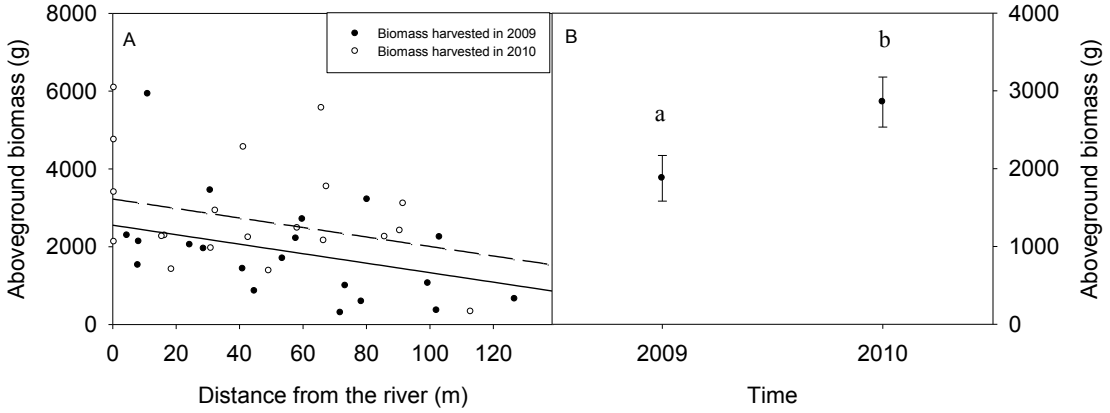

Figure 2.2. Relationship between aboveground biomass and distance from the river (A) and two year comparison (B). (A) For 2010, Biomass = 3539.8 – 15.4 × distance from the river ($p = 0.012$, $R^2 = 0.26$). Error bars represented the standard error. Aboveground biomass was collected at the end of summer growing season in Aug 2009 and 2010. Dashed line was the linear regression line for harvested in 2010 and solid line was for 2009.

Aboveground biomass was on average 30% higher in 2010 across the floodplain (Figure 2.2) compared with 2009, suggesting 2010 had better growth conditions ($p < 0.05$). In both years, aboveground biomass decreased as distance from the river increased. Within the 100-m-wide riparian zone, aboveground biomass was estimated to decrease by about 1500 g from the river inland (Figure 2.2). Aboveground biomass was not related to elevation gradients.

Belowground biomass consisted of rhizomes and roots, both of which were not affected by distance from the river or relative elevation ($p > 0.05$, data not shown). The top 20-cm soil layer contained 98.8% (4.6 kg/m^2) of total belowground biomass, which decreased rapidly with soil depth. In addition, the rhizomes appeared sporadically in the samples.

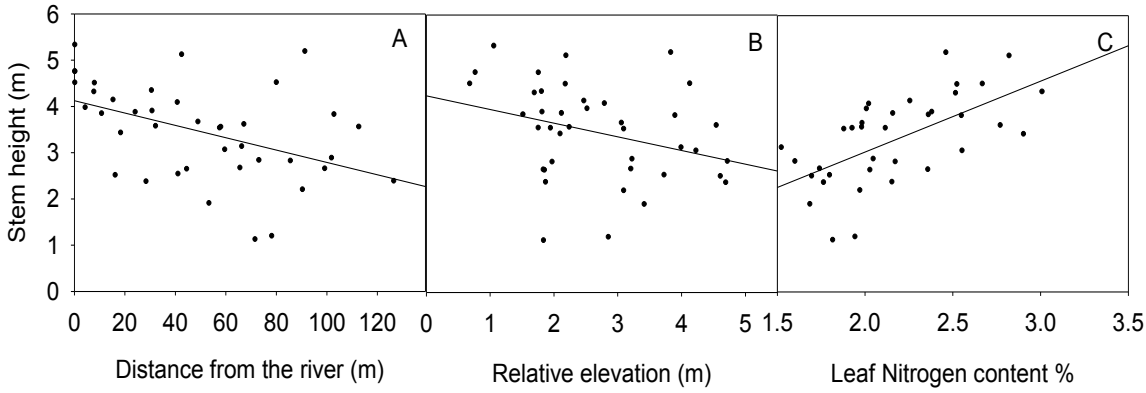

Figure 2.3. Linear relationships between stem height and distance from the river (A), relative elevation (B), and leaf nitrogen content (C). (A) Stem height = 4.1 - 0.013× distance from the river, $p = 0.0029$, $R^2 = 0.2$. (B) Stem height = 4.25 - 0.296 × Relative elevation, $p = 0.0.04$, $R^2 = 0.10$. (C) Stem height = -0.04 + 1.54 × leaf nitrogen, $p < 0.0001$, $R^2 = 0.38$.

Stems were shorter further away from the river and groundwater (Figure 2.3 A and B). In addition, taller stem exhibited higher leaf nitrogen (Figure 2.3 C). However, stem density was not affected by distance and elevation gradients.

Consistent with my second hypothesis, water availability was tightly linked to floodplain geomorphology and soil texture gradients. Each of the four transects had a distinct pattern in relative elevation with distance from the river (Figure 2.4 A). As expected, soil moisture decreased as the relative elevation increased (Figure 2.4 B).

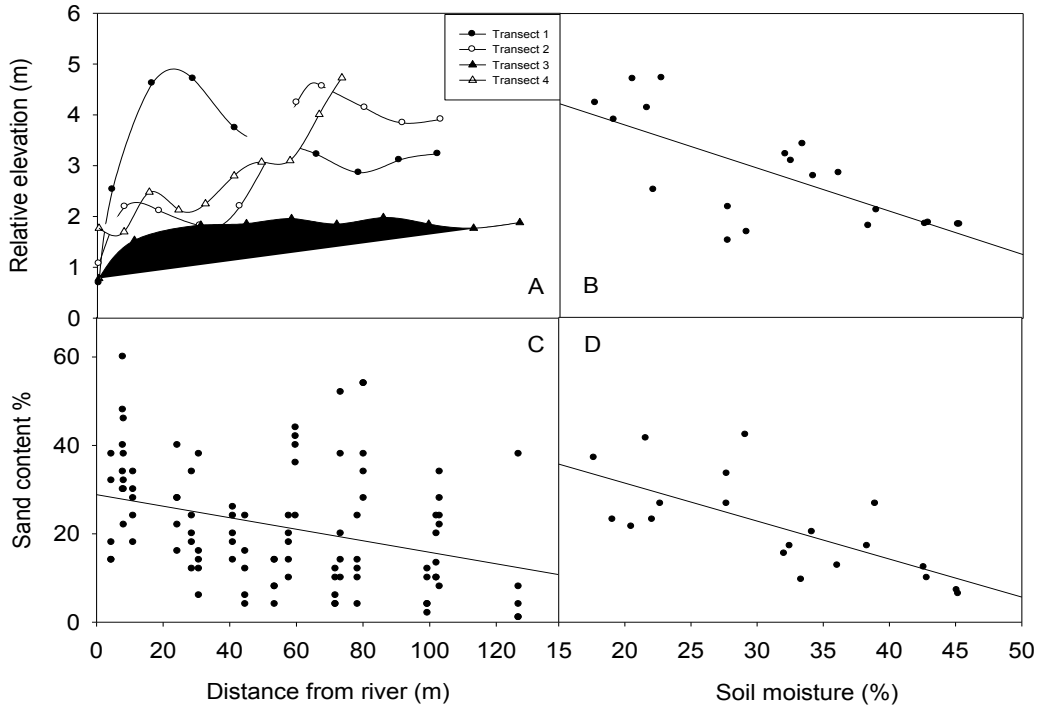

Figure 2.4. Relationship among relative elevation, soil texture, distance from the river, and soil moisture. (A) Relative elevation changed in 4 transects. (B) Linear relationship between two-year average soil moisture and relative elevation (n = 20). Soil moisture = 48.6 - 6.05× relative elevation, p = 0.0004, R^2 = 0.51. (C) Variation of sand content at all 20 cm increment depth in response to distance (n=100). Sand content = 28.9 - 0.13 × distance from the river, p = 0.0005, R^2 = 0.12. (D) soil texture changed in relation to two-year average soil moisture (n=20). Soil moisture = 43.8 - 0.58 × sand content, p = 0.0005, R^2 = 0.50.

Soil was coarser close to the river edge (Figure 2.4 C). Larger soil particles were accumulated at river edge, which can retain less soil moisture (Figure 2.4 D). However, the distance from the river increased, the soil moisture did not differ with increasing clay content ($p > 0.05$). Finer soil apparently had better nitrogen holding capacity, given the increase in soil nitrogen with distance and elevation (Figure 2.5 A, B).

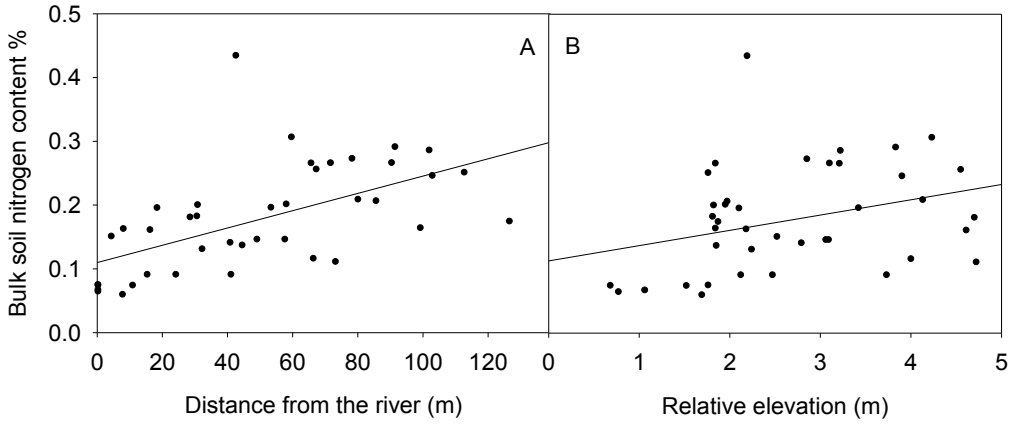

Figure 2.5. Variation of top 20-cm soil nitrogen content in response to distance from the river (A) and relative elevation (B). (A) Soil nitrogen = 0.11 + 0.0014 × distance from the river, $p < 0.0001$, $R^2 = 0.33$. (B) Soil nitrogen = 0.11 + 0.02 × relative elevation, $p = 0.044$, $R^2 = 0.10$.

DISCUSSION

This research focused on the ecohydrological controls on the performance of invasive species *Arundo donax* growing along the Rio Grande. It revealed that performance of this clonal riparian invasive species was influenced by gradients in water availability associated with floodplain geomorphic features.

The performance of *A. donax* adversely responded to both drought and inundated conditions. Short-term plant performance is regulated by stomatal conductance, which can remain constant within a range of soil moisture. When water availability becomes too low (drought) or too high (flood), stomatal conductance decreases (Lambers et al. 1998). Thus, performance of *A. donax* increases with water availability within a certain range and decreases when the water availability crosses a "peak-point" (Everitt 1998).

Even though groundwater depths tend to be shallow in riparian environments, soil moisture in the top 1 m still is an important factor determining the success of this clonal plant. Streamside clonal vegetation growth patterns is strongly correlated to soil moisture gradients for many riparian species (Auble et al. 1994, Prach and Pysek 1994, Stromberg et al. 1996, Naiman and Décamps 1997, Dwire et al. 2004, Souza and Martins 2004, Gomes and Asaeda 2009). With regards to *A. donax*, the phenomenon of increasing plant photosynthesis, leaf carbon stable isotope ratio, and aboveground biomass is related to higher, but not saturated soil water condition. Under these conditions, *A. donax* can maximize its photosynthesis and produces larger amount of carbohydrates, which can increase the survival and growth of this species. This is also consistent with other research that soil moisture might be the primary factor in regulating rhizome sprouting (Boose and Holt 1999) and overall growth responses (Decruyenaere and Holt 2001).

Given that roots of *A. donax* can grow at least 4.8 m (personal observation) and extend below the water table, it is very likely that plants switch water source from mainly upper soil to groundwater when the top soil gets dry. For example, *Prosopis velutina*, although it is not a clonal herbaceous plant, shifts between groundwater and soil moisture in response to changing climate and water availability (Snyder et al. 1998). As a result, precipitation is unlikely to have had a strong impact on the ability of well-established population of *A. donax* to obtain water (Decruyenaere and Holt 2005).

Over longer time scales of a growing season, I observed uniformity of biomass and stem density across resource gradients, but stem height decreased. The variations of

plant structural traits associated with environmental changes suggests that *A. donax* exhibits clonal plasticity (Bradshaw 1965). As observed in the *A. donax*, at higher elevation with less access to groundwater and soil water, stems were shorter and leaf nitrogen content was lower. This has been consistent with Spencer's findings that leaf N was lower in the plants that were further away from the water (Spencer et al. 2005), which indicated N may be a secondary influencing factor. However, if the nitrogen is abundant on the floodplain (Spink et al. 1998, Drinkard 2009), it is possible that leaf N content was controlled by plant performance, whereby clones invest more carbohydrate but less nitrogen per unit mass in the leaves when water access is limited. The increasing allocation to plant structure materials is likely to decrease plant function; however, it requires less energy and extends leaf longevity. Future research is needed to determine the role of nitrogen in controlling plant performance in riparian zones.

Although *A. donax* favors ample soil moisture, it also exhibited signs of stress during flooded or saturated soil conditions. Plants commonly decrease productivity in response to flooding (Robertson et al. 1978, Frye and Quinn 1979, Hupp and Osterkamp 1985, Stromberg and Patten 1990, Auble et al. 1994, Bell 1997, Patten 1998) because when soil is saturated, oxygen supply to roots is likely limited. Plants respond to anaerobic soil conditions by reduced stomatal aperture, transpiration, and absorption of water (Kozlowski 1984). Thus, flooding can adversely affect the growth of plants from many aspects, such as leaf initiation and root growth. For example, flooded condition limited growth and clonal propagation of *Phragmites* (Amsberry et al. 2000, Xiao et al. 2011). Even though ultimately biomass was greater in 2010 than it was in 2009, high

rainfall and flooding in 2010 reduced photosynthesis temporarily. Boose and Holt (1999) also evidenced that reproduction of *A. donax* was strongly limited by water logged conditions.

Ultimately, geomorphology controlled all of the gradients observed in this study. Spatially, soil moisture was negatively related to relative elevation either because of closer proximity to the capillary fringe zone (Chen and Hu 2004) or because higher elevations were well-drained. Hydraulic sorting of Rio Grande sediments results in different particle size distribution on the floodplain: the coarse soils were deposited along the river edge, while the finer soils were accumulated further from the water course. The soil texture gradient formed by sediment deposits seemed to determine maximum soil water holding capacity (Rossa et al. 1998, Kirkham 2005). Soil texture trends were consistent with other studies that found sediment on the streamside was generally coarser relative to upland (Frye and Quinn 1979, Osterkamp and Hupp 1984), which can potentially affect plant growth or distribution pattern (Ware and Penfound 1949, Frye and Quinn 1979). Coarse soil also tends to have less nitrogen holding capacity (Taiz and Zeiger 2010). In my study, soil texture tended to counteract the effects of distance from river and relative elevation, which enhanced the uniformity of vegetation performance to some extent across the elevation gradients.

On the other hand, coarser soils may have better drainage in the frequent flooding areas. Better oxygen diffusion in the coarse soil can increased plant root respiration and support plant to grow vigorously. Previous studies suggested that *A. donax* performs better in sandy soils (Spencer et al. 2008, Ceotto and Di Candilo 2010)

that are well-drained (Hoshovsky 1989). Therefore, it is likely that *A. donax* growing in the sandier soil may have better root respiration to support the vigorous growth observed close to the river.

In conclusion, performance of *Arundo donax* is likely affected by water availability including soil moisture and groundwater access. However, mature patches can tolerate a wide range of moisture (from wilting point to saturated soil) and maintain a high level of production via its plasticity in water use efficiency (Christou et al. 2003). In addition, *A. donax* might be a drought avoider due to development of long extending roots, which allows plants to take up groundwater when soil gets dry. Clonal plant plasticity, water use efficiency, and clonal integration (refers to Chapter III) can potentially ameliorate impacts of water stress on plant growth and performance and improve adaption to the heterogeneous riparian environment. Furthermore, geomorphology controls environmental gradients and ultimately results in a resource-abundant riparian zone and further enhances uniform growth of *A. donax*. This study reinforces the importance of measuring integrative environmental variables that incorporate the relative elevation and soil water content when evaluating clonal plant performance in arid and semiarid riparian ecosystems. Future research is needed to determine the role of clonal integration in ameliorating drought responses along environmental gradients.

CHAPTER III

CLONAL INTERGRATION OF *ARUNDO DONAX* IN THE RIPARIAN ZONE

INTRODUCTION

Many clonal plants can remain interconnected belowground, which may allow for physiological integration: the translocation of water resources, nutrients, or carbohydrates from a larger "mother" ramet to a developing "daughter" ramet (Marshall 1990, Caraco and Kelly 1991, De Kroon et al. 1998). Physiological integration among clones can significantly improve the survival rate of a local population (Brezina et al. 2006), enhance fitness (Peterson and Chesson 2002), and support the growth of ramets into harsher environments (Xiao et al. 2010).

To date, research focused on a variety of clonal plants has determined that the extent of physiological integration differs among species (Williams and Briske 1991), size of ramet (Brezina et al. 2006), and resource availability (Caraco and Kelly 1991, Charpentier et al. 1998, Pauliukonis and Gough 2004). Individual ramets of *Schizachyrium scoparium* were physiologically independent and become physically detached early (Derner and Briske 1999), while rhizomes of *Carex* species remain connected for a lifetime (De Kroon et al. 1996). The direction of resources sharing among *Carex* rhizomes (parent to daughter, or daughter to parent) depends on the location of sources or sinks within the clone (De Kroon et al. 1996).

Clonal integration evidenced within a given species can differ, for example, at different rooting stages (pre- and post-rooting stages) or under local environmental

conditions (heterogeneous and homogeneous). Typically, connections between ramets are active before the youngest ramets root (Matlaga and Sternberg 2009). Connections between ramets can also result in resource sharing when there is a strong resource gradient, i.e. if ramets growing in dry or poor nutrient environments are connected with neighboring ramets growing in resource-abundant habitats (De Kroon et al. 1998, Fischer and Van Kleunen 2001, Pauliukonis and Gough 2004, Matlaga and Sternberg 2009). In a *Calathea marantifolia* experiment, daughter ramets grown in pots with low nutrient and water availability were able to obtain and consume resources from their mother ramets grown in resource-sufficient pots (Matlaga and Sternberg 2009).

Clonal integration may play an important role in the success of exotic and/or invasive species (Prach and Pysek 1994). Because physiological integration allows clonal plants to exploit ephemeral resources and patchy substrates, invasive clonal plants may have an advantage over non-clonal plants in some resource-poor habitats. In particular, in riparian habitats, taking advantage of river water and nutrients available on the banks and distributing those resources throughout the floodplain may allow some clonal invasive plants to grow faster and expand more rapidly than the non-clonal native plants (Cushman and Gaffney 2010). *Spartina alterniflora*, which invades along the coastal region of China, is widespread due in part to its physiological integration (Xiao et al. 2011). For the same reason, *Phalaris arundinacea*, a common wetland invader in North America, has greatly impacted native communities (Maurer and Zedler 2002).

Stable isotope methods are powerful tools for improving understanding of the relationships between plants and their environments, such as in the field of plant ecology

(Robinson et al. 2000, Dawson et al. 2002) and ecohydrological research (Busch et al. 1992, Darrouzet-Nardi et al. 2006). Deuterium labeled water in particular has been used to trace water movement between ramets and understand their resource sharing (Cline 1996, De Kroon et al. 1996, Hay and Newton 1996, Turnbull et al. 1997, De Kroon et al. 1998, Matlaga and Sternberg 2009). De Kroon et al. (1996, 1998) applied a deuterium tracer to pots to study water translocation between interconnected mother and daughter ramets. There are two key benefits of applying labeled water as a tracer. First, applied enriched water can be detected more easily as it becomes diluted in the rhizome network (Reyes-Garcia and Andrade 2007), because its signal is distinct from the range of natural variation caused by evaporation or condensation. Second, there is no isotopic fractionation of deuterium enriched water during plant water uptake (Wershaw et al. 1966, Reyes-Garcia and Andrade 2007).

While stable isotope methods have been used to confirm and quantify resource sharing among ramets, rhizome severing experiments are used to investigate potential ecological benefits of clonal physiological integration (Railing and McCarthy 2000, Pauliukonis and Gough 2004). In these experiments, plants whose rhizomes are severed are compared with intact plants on their survival rate and growth-related parameters such as ramet biomass and height. Dong and Alaten (1999) severed *Psammochloa villosa* rhizomes and found that all the growth-related parameters were reduced compared to the controls. Wang et al. (2004) compared the growth of ramets and rhizomes when they were attached and detached from *Leymus chinensis* (Trin.) rhizomes. They found that rhizome severing had no effect on any tested variables. Research on *Scirpus maritimus*

suggests that severed rhizomes can produce more ramets (Charpentier et al. 1998); however, another study on *Solidago canadensis* found severed rhizomes restricted the propagation of the new ramets (Schmid and Bazzaz 1987).

This study focuses on an invasive riparian reed grass, *Arundo donax* L., a clonal plant of the family *Poaceae* that is widely distributed in North America (Decruyenaere and Holt 2001). Similar to many clonal plants, it has robust persistent rhizomes and propagates solely by vegetative means, expanding from horizontal root stocks, rhizomes, or growing from stem fragments (Van Groenendael et al. 1996, Dudley 2000, Spencer and Ksander 2006).

There are several reasons for selecting *Arundo donax* to study clonal integration. First, it exhibits many of the characteristics of a typical invader, such as rapid growth rate, high productivity, community dominance, and good tolerance of a wide range of environmental conditions. Many of these advantages can be attributed to clonal integration. Second, *A. donax* typically invades semi-arid riparian ecosystems, where evapotranspiration often exceeds annual rainfall (Weltz and Blackburn 1995, Wilcox et al. 2006). If *A. donax* uses clonal integration to transport river water over longer distances than would be accessed by native non-clonal plants, then water supplies might be impacted. Third, studying new pathways for water movement in riparian environments can improve our knowledge of plant transpiration and water budgeting in this type of ecosystem. Riparian environments typically switch from homogeneous-wet to strong wet-to-dry gradients, quite possibly *Arundo donax* can take advantage of wet conditions and transport resources to their neighbor ramets on the floodplain terraces.

On the other hand, it may not be necessary for *A. donax* to maintain physiological integration. Given that *A. donax,* rhizomes can reach up to 40 cm in length and 10 cm in diameter, storage of water within belowground structures may sustain growth during brief drought (Knapp and Fahnestock 1990). Likewise, *A. donax* roots can penetrate to about 5 meters (personal observation), which in many riparian areas may provide access to groundwater. Matlaga and Sternberg (2009) concluded that resource sharing did not exist when ramets grew in homogeneous resource-abundant conditions, because it was costly to maintain integration if the plant can take up the resources locally. One study in particular assumed *Arundo donax* used clonal integration but did not have direct evidence of this (Cushman and Gaffney 2010). Although *A. donax* maintains rhizome connection between ramets, it is not known whether physiological integration is involved in this plant's growth strategy.

Most of the studies mentioned above for several clonal plant species have been done under controlled conditions (pots and green houses) and with short clonal fragments consisting of a few ramets, except that Dong (1999) manipulated the rhizomes in a severing experiment on natural populations in the field. These are important experiments that yield insights to clonal plant growth. However, applying those experiments in naturally-populated habitats may improve our understanding of plant feedback under realistic environmental conditions and over greater distances with potential for interaction among soil, water, and nutrients (refer to Chapter II).

I applied an isotope labeling experiment and a rhizome severing experiment to examine the existence and potential benefits of clonal integration in *Arundo donax* on

the floodplain of lower Rio Grande River. This effort has two major questions. The first is to determine whether *Arundo donax* shares resources (here water) through the interconnected rhizomes. If clonal integration exists, the second question is to determine by how much it contributes to demography and growth of *Arundo donax*.

A deuterium labeling experiment was designed to answer the first question, while the rhizome severing experiment was designed primarily to answer the second question, but with the potential to substantiate the previous question as well. I hypothesized that *Arundo donax* exhibits clonal integration and it can increase the recruitment and growth of the plant.

MATERIALS AND METHODS

Site Description

Research sites were located on the floodplain of the lower Rio Grande River (29°14' N, 100°47' W), in areas of nearly monoculture stands of *Arundo donax* with sparse honey mesquite (*Prosopis glandulosa* Torr.). The growing season of *A. donax* extends from March to December of most years. The elevation of the floodplain at our study site is around 258 m above sea level.

The mean annual precipitation is 477 mm $year^{-1}$ and monthly average temperatures range from 10 °C in winter to 27 °C in summer (NOAA 2010b). In July 2010, this area experienced a significant flood event. The total precipitation from June to August was 33 cm in 2010, twice the rainfall amount compared with 30-year averages for those months (NOAA 2010a). The flood partially inundated my experimental plots for the period of July 7th through July 15th because of significant releases from Amistad

Dam at Del Rio, TX and local precipitation. After the flood, the river continued to flow at higher than normal levels until late August 2010.

Sites for the rhizome severing experiment and deuterium labeling experiment were near transect 2 (refer to Chapter II for transect descriptions). Both experiments were conducted in the summer 2010, beginning at the end of May through the middle of August.

Rhizome Severing Experiment

This experiment was conducted along transect 2 on the floodplain, as shown in Figure 3.1.

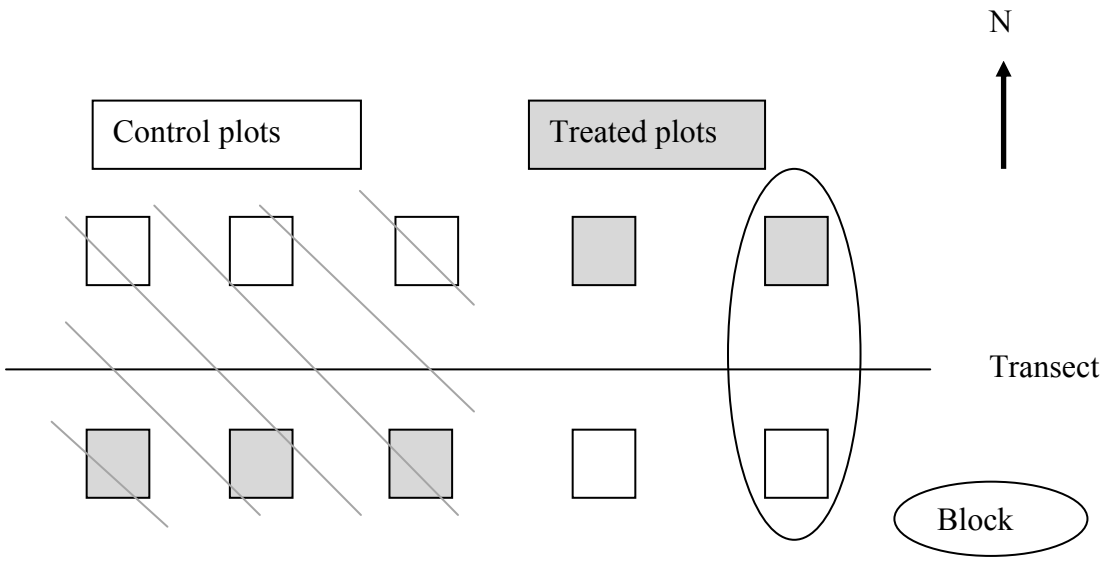

Figure 3.1. Diagrammatic representation of rhizome severing experiment. The solid grey plots were treated plots and others were control plots. Plots with diagonal were inundated for approximately 10 days during flooding.

A randomized complete block experimental design (Ott and Longnecker 2010) was used to account for potential environmental gradients, such as soil moisture, that exist along the transect. Each block consisted of a pair of plots at equal distances from the river. Five 1×1 m^2 paired experimental units (plots) were established 8-m away from each other and 3-m besides existing study plots 0, 2, 4, 6, and 8 (Figure 3.1, see also Chapter II for plot descriptions).

On May 31st and Jun 1st, we removed stems from all the plots by clipping the aboveground biomass. Stem basal diameters (approximately 2 cm above the soil surface) were measured using calipers with a precision of 0.1 mm. Then, stem heights were recorded to the nearest 1 cm, and the number of stems per plot was counted to document initial conditions prior to treatment. Plant materials were dried in the oven at 60 °C to a constant weight. Total plot biomass was determined from dry weight.

To test for potential differences in plant growth with and without resource sharing, rhizomes were severed in one plot randomly selected from each pair of plots in the block while rhizomes were left intact in the other (Figure 3.1). Rhizome severing took place on June 2nd as follows. Using a saw blade, I severed underground rhizome connections around the perimeter of all plots selected for treatment to the depth of 30 cm. In the control plots, I disturbed the soil at the perimeters of plots using the same method only without severing the rhizomes. The reason for soil disturbance in both plots was to account for any effects on plant performance caused by the disturbance. All soil and litter were moved back into place after rhizome severing or soil disturbance.

Three weeks (Jun 21st), seven weeks (Jul 20th), and eleven weeks (Aug 18th) after rhizome severing, the stem heights and basal diameters of regrowth were measured and stem numbers were counted. At the eleventh week, besides measuring plant growth-related characteristics described above, live stems were harvested at the ground surface and dry weights of final aboveground biomass were determined with the same procedure as used for the initial harvest.

The transect was partly inundated by the flood for about eight days between Jul 7th and Jul 15th, in particular west direction of 3 entire blocks (Figure 3.1).

Deuterium Labeling Experiment

Deuterium enriched labeled water ($\delta^2H \sim 1800$ ‰) was applied to *Arundo donax* plots as a tracer, approximately following the methods of Matlaga and Sternberg (2009). The experiment was conducted on a naturally-populated, continuous monoculture of *Arundo donax* in the center of floodplain, approximately 100 m from the water course. There was no elevation gradient in the research site; therefore, I assumed that water applied on the plants primarily percolated downward instead of flowing horizontally in any direction.

After the flood subsided and 20 days passed without precipitation, we started the experiment on Aug 16th, 2010. Three 1-m-diameter plots as shown in Figure 3.2 were set up 10-m apart. Before watering, rhizome and soil samples were collected for background isotopic determination. In each plot, 5 sample points on the 4-m ring were randomly picked for rhizome and soil samples collection. At each sample point, rhizome samples approximately 5-mm diameter and 10-mm long were collected using an increment borer.

Soil background samples were collected from the upper 10 cm adjacent to each rhizome. To minimize evaporative isotopic fractionation, soil and rhizome samples were sealed in scintillation vials with Polyseal cone caps (Qorpak, Bridgeville, PA) followed by parafilm sealing to prevent cap loosening immediately after collection. Then all the samples were kept in the shade until moved into the freezer (-4°C) at end of the day. Samples stayed in the freezer until water extraction.

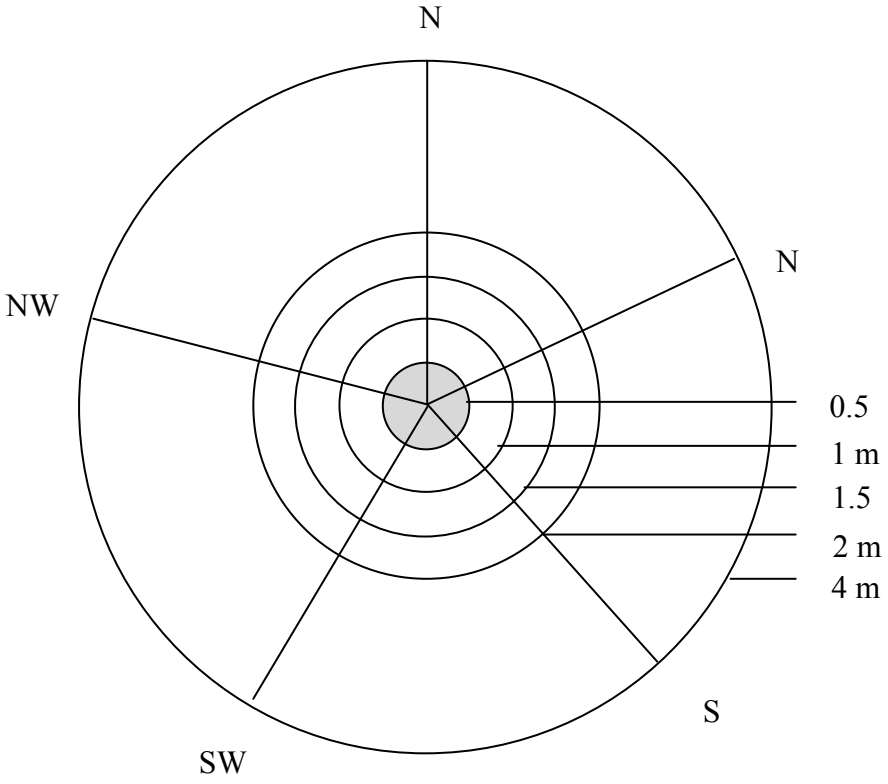

Figure 3.2. Diagrammatic representation of one of the plots for watering experiment. The center dark color was 1-m diameter watering area. Rings outside the watering area identified 4 distances to the center of the labeled ramets, 1 m, 1.5 m, 2 m, and 4 m. Five direction lines (N, NE, NW, SE, SW) started from the center of watering area and ended at 4-m ring.

After collecting the background samples, 18.4 L of deuterium-enriched water was sprayed inside the 0.5-m watering area on each plot over the course of 30 minutes to avoid any overflow outside the watering area. Soil was sandy and water penetrated quickly without ponding on the surface. For every plot, the watering process was repeated on three successive days between 8 am and 10 am (Aug 16th through 18th). To simulate natural rainfall conditions, the amount of water (18.4 L × 3 days) sums to 55.2 mm, which was approximately the 30-yr mean rainfall for the period between June and August. A single rainfall event can be up to 431 mm (e.g., August 23rd, 1998) (NOAA 2010a). The assumption was that roots in the water zone were primarily connected to rhizomes directly above them. It is possible to overestimate rhizome transport if some labeled water moved through other pathways.

To trace the movement of deuterium water between donor ramets in the zone of applied water and recipient ramets at distances beyond the applied zone, 25 rhizome samples and 3 soil samples were collected at 5 hours, 24 hours, and 48 hours after the last day of watering (August 18th, 19th, and 20th, respectively) from each plot and stored using the same procedure as for background sample collection. The location of rhizome sample collection takes into account the distance from the watering area and the direction from the watering center. As shown in Figure 3.2, there were 5 rhizome samples taken from each ring at 0.5, 1.0, 1.5, 2.0, and 4.0 m, corresponding to 5 cardinal directions. Differently, for the 0.5-m-ring rhizomes, the samples were collected within the watering area instead of on the ring boundary. Three additional surface soil samples were collected within the watering area at the beginning (Aug 18th) and end (Aug 20th)

of the experiment. In addition, soil samples were collected at three depths (10 cm, 20 cm, and 30 cm) within the watering area on Aug 19th.

Samples were processed at Texas A&M University for water extraction and determination of deuterium content. Water from soil and rhizome samples was extracted using the cryogenic vacuum distillation method (West et al. 2006). A vial of reference water of a known isotopic composition was placed in the fridge every day after extraction to correct for potential evaporation effects during the water storage.

Groundwater was collected from nearby wells located at plot 1 and plot 9 of transect 2 every month (June 7th, July 20th, and August 13th). The hydrogen stable isotope ratio of groundwater samples along with water extracted from soil and rhizome samples for the labeling experiment were analyzed on a Delta V Isotope Ratio Mass Spectrometer coupled to a High Temperature Conversion Elemental Analyzer (TC/EA-IRMS; Thermo Fisher Scientific, Waltham, MA).

The hydrogen stable isotope ratio for a sample was expressed in delta notation (δD) in parts per thousand (‰) relative to the internationally reference standard, Standard Mean Ocean Water (SMOW) (Dawson et al. 2002):

$$\delta D_{sample}\,(‰) = (R_{sample} / R_{standard} - 1) \times 1000\ ‰$$

where R_{sample} and $R_{standard}$ presented D/H ratio in the sample and standard, respectively. The δD value of the labeled water was ~ 1800 ‰, which was mixed by 53.5 mL of 99.95% heavy water (D_2O) and 170 L local tap water.

A mass balance mixing model can be used to calculate the water source or sources for terrestrial plants from water collected in their rhizomes compared with water

collected from potential sources (Dawson et al. 2002). I used δD to estimate the proportion of plant water uptake from the simulated precipitation event based on δD value of rhizomes, surface soil water, and groundwater. The fractional water uptake F was calculated from δD_A, equal to δD of soil samples in the top 10 cm at ten minutes after watering, and the initial δD_B, equal to the δD value of groundwater, which was another end member of the mixing model:

$$F = (\delta D_{rhizome} - \delta D_B) / (\delta D_A - \delta D_B)$$

where F is the proportion of surface water present in the rhizomes after watering (Balesdent et al. 1987, Amelung et al. 2008, Fuentes et al. 2009). Although the deuterium content in groundwater was quite constant, δD of soil samples across the soil profile varied with depth because of evaporative enrichment. The δD value of soil within the top 10 cm where the rhizomes were located represented one constant source and ground water represented another one. As a result, we can estimate the minimum fraction of water that plants obtained from the surface soil; although, it is difficult to estimate the exact fraction of water that individual plants acquired from our simulated rainfall event (Darrouzet-Nardi et al. 2006).

Statistical Analyses

All data were analyzed in JMP v.8 (SAS Institute, Cary, North Carolina). Since the data were not normally distributed and non-homogenous variances were too extreme to be normalized using data transformations, I used non-parametric method through rank transformation of the dependent variables (Ott and Longnecker 2010) in both experiments. However, the text and figures presented unranked means and standard

deviations. The F-statistic in all statistical analysis was considered significant at $\alpha = 0.05$.

For the rhizome severing experiment, I used a standard randomized block design. Treatment effects were evaluated using a two-way ANOVA with treatments (severed and control treatment) and block (1 through 5) as the grouping factors (Ott and Longnecker 2010). Stem density, aboveground biomass, stem diameter, and plant height were response variables. Block was treated as a random effect in all analyses and I did not calculate the effect of treatment × block because I didn't replicate within each block.

For the deuterium labeling experiment, I used ANOVA with four-way interaction: plots, directions, days of sampling, and distances from the watering plots. The δD of rhizomes were response variable (Ott and Longnecker 2010). Reciprocal regression was used to find out the relationship between the distance from the center of watering area and δD of rhizome water. In the meantime, δD of rhizomes after watering were also analyzed using geostatistics, ArcGIS v 9.2 (ESRI, Redlands, CA) to visually analyze the difference between three plots across three days. Kriging, a method of interpolation between sampled points based on the spatial autocorrelation between distance and deuterium signal at the sample points (Kent et al. 2006).

RESULTS

Rhizome Severing Experiment

Prior to the experiment, initial conditions were similar among paired plots in terms of plant height, stem diameter, aboveground biomass, and plant density ($p > 0.05$;

Table 3.1). However, those factors differed between plot pairs along an environmental gradient. New stems sprouted in all the plots one week after treatment.

Table 3.1. The mean values (±1 SD) for stem density, stem height, and stem diameter for the Jun 1st, Jun 21st, Jul 20th, and Aug 18th. T and C in the treatment column mean treated plots and control plots, respectively. The shaded row was presented initial condition. The bold numbers stand for significant difference between control and treated plots. There was no aboveground biomass harvest in the weeks of Jun 21st and July 20th.

Day	Treatment	Stem density	Plant height (m)	Stem diameter (mm)	Aboveground biomass (g)
Jun 1st (Pre-experiment)	T	21.6±3.8	3.5±0.8	15.6±4.0	2868±1501
	C	20.8±9.7	3.5±0.4	16.4±2.0	2855±1326
Jun 21st (week 3)	T	**14.2±7.9**	0.35±0.1	10.5±2.1	--
	C	**7.2±6.1**	0.52±0.1	10.9±3.8	--
Jul 20th (week 7)	T	7.8±2.9	1.75±1.0	11.6±3.4	--
	C	5.6±4.8	2.18±0.8	11.9±4.1	--
Aug 18th (week 11)	T	6.4±3.7	**1.92±0.9**	**8.9±2.6**	816 ±1031
	C	5.6±5.9	**3.2±0.4**	**13.3±3.2**	732.2±703

Contrary to the hypothesis, after the first three weeks, rhizome severing actually increased the recruitment of new *Arundo donax* by 98%, compared with plots whose rhizomes were left intact (Table 3.1). However, stem diameter and plant height during the 3rd week was the same, whether rhizomes were severed or not (Table 3.1, Figure 3.3).

On July 20th, by seven weeks after rhizome severing, more stems had died in the severed plots than in the plots with rhizomes intact such that all growth-related parameters of ramets were equal among all paired plots ($p > 0.05$, Table 3.1). During the

period of flood, which occurred after 3 weeks but before 7 weeks into the experiment, 42 ± 13% of plants with severed rhizomes were dead compared with only 20 ± 21% of the plants with intact rhizomes. Therefore, rhizome severing was associated with higher stem mortality after flooding ($p = 0.072$).

By Aug 18th, eleven weeks after rhizome severing, plants with intact rhizomes had grown bigger and taller than their severed counterparts (Table 3.1, Figure 3.3). Individual plants with intact rhizomes were 67% taller and 49% larger in diameter than their severed counterparts. This finding was consistent with our hypothesis that ramets will grow better with the support of neighboring ramets. However, plant density and aboveground biomass were similar ($p > 0.05$). In summary, as shown in Figure 3.3, over the 11 weeks of growing season, rhizome severing increased the propagation of new ramets at first, but also increased the mortality of ramets by the end of the experiment.

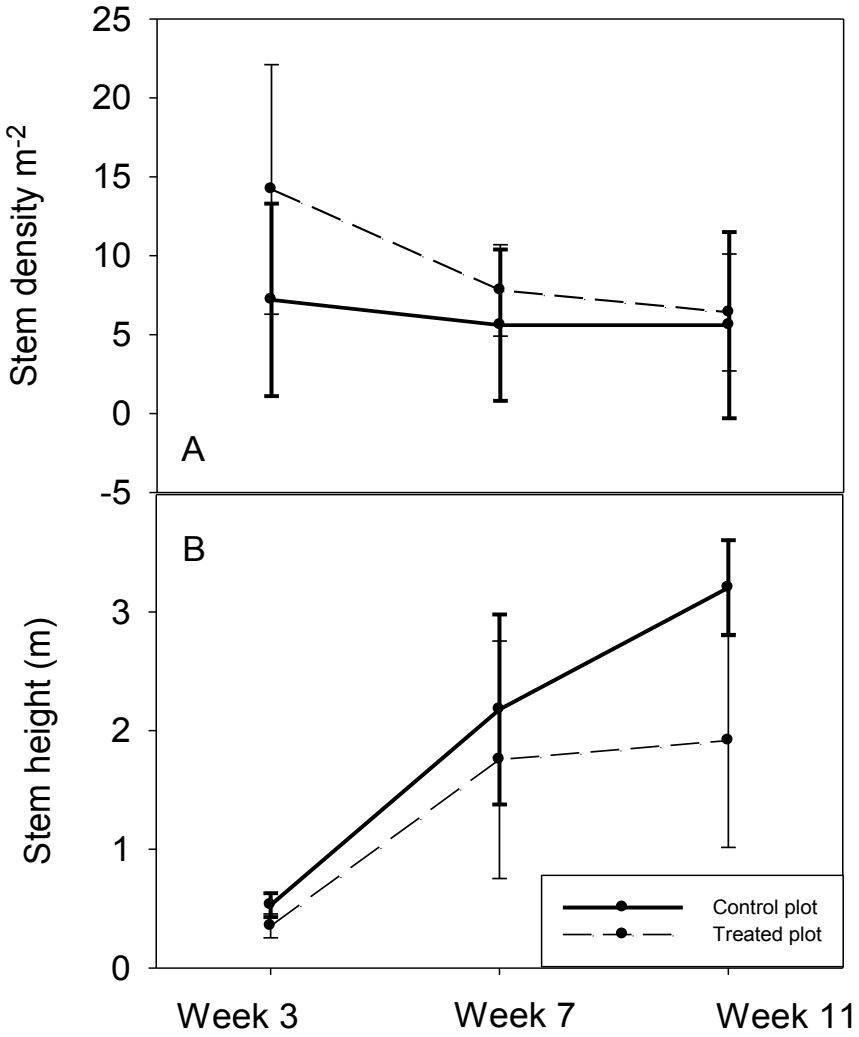

Figure 3.3. The stem density (A) and stem height (B) changed between plots with rhizome severing and intact over the period of 11 weeks. Error bars stand for standard deviation.

Deuterium Labeling Experiment

Prior to watering, the δD of background rhizomes water and soil samples were -28 ± 3.5 ‰ (mean ± standard deviation), ranged between -34‰ to -20‰. Isotopic composition of rhizomes and soil did not differ ($p > 0.05$).

The labeling protocol was effective. After applying deuterium enriched water, the δD of soil inside the watering area within 10-cm from the surface increased to 1481 ± 258 ‰. δD values of soils gradually decreased with depth, where δD at 30-cm deep was a mean of 147‰. As the water percolated into the soil profile, it was depleted in deuterium by dilution with pre-existing water in the soil along its path.

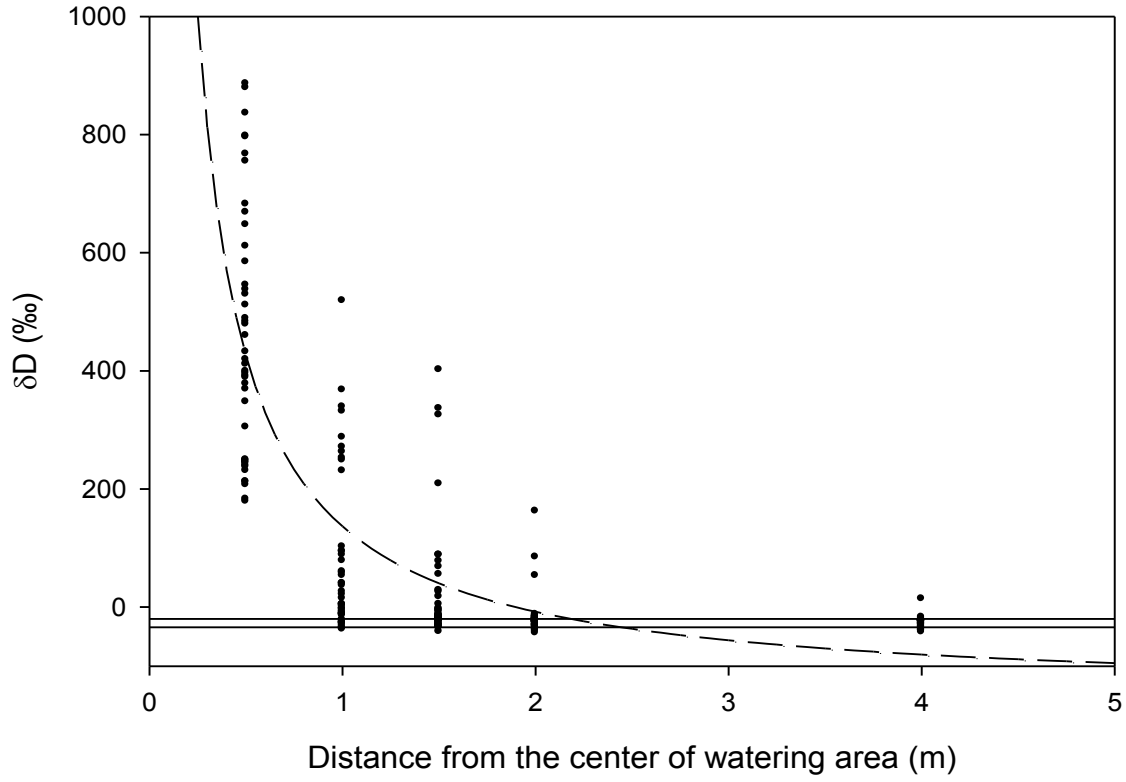

Figure 3.4. δD (‰) of rhizome samples observed at different distances to the center of the watering area. The bottom two lines indicate the background range of between -20‰ and -34‰. Dashed was estimated relationship between δD and distance (δD = -152.9 +289.5/distance from center, R^2=0.66).

Deuterium content in the rhizomes rapidly decreased with increasing distance from the watering area (Figure 3.4, Table 3.2). The fitted equation was δD = -152.9

+289.5/distance from center, R^2=0.66. According to this relationship, δD was estimated to drop into background range at 2.17 m from center of watering area (or 1.67 m from the edge). By 30 cm distance, the signal had dropped 50%. Within the watering area (inside 0.5 m), the mean deuterium content of rhizomes was 457‰ and ranged from 179‰ to 886‰. Importantly, any rhizome whose δD value was higher than the background value indicated at least some uptake of the labeled water. At 2-m distance, 3 out of 45 samples were higher than the general background signal. At 4-m, one (+14‰) out of 45 samples was higher than the background signal.

Direction of samples and sampling days did not affect the variation of deuterium concentration in the rhizomes (Table 3.2, Figure 3.5). Plants took up water from top soil at a constant rate between 3-5 days and apparently transported the water along the rhizomes equally in all directions.

Table 3.2. The effects of distance to the center, plot location, direction of samples, and sampling days on the δD of rhizomes. Asterisk mean the dependent variable changed significantly as independent variables changed.

Source	**DF**	**F Ratio**	**Prob > F**
Distances from center	4	182.4853	<.0001*
Plots	2	13.7468	<.0001*
Directions	4	0.3484	0.7266
Days of sample collection	2	1.2413	0.3924

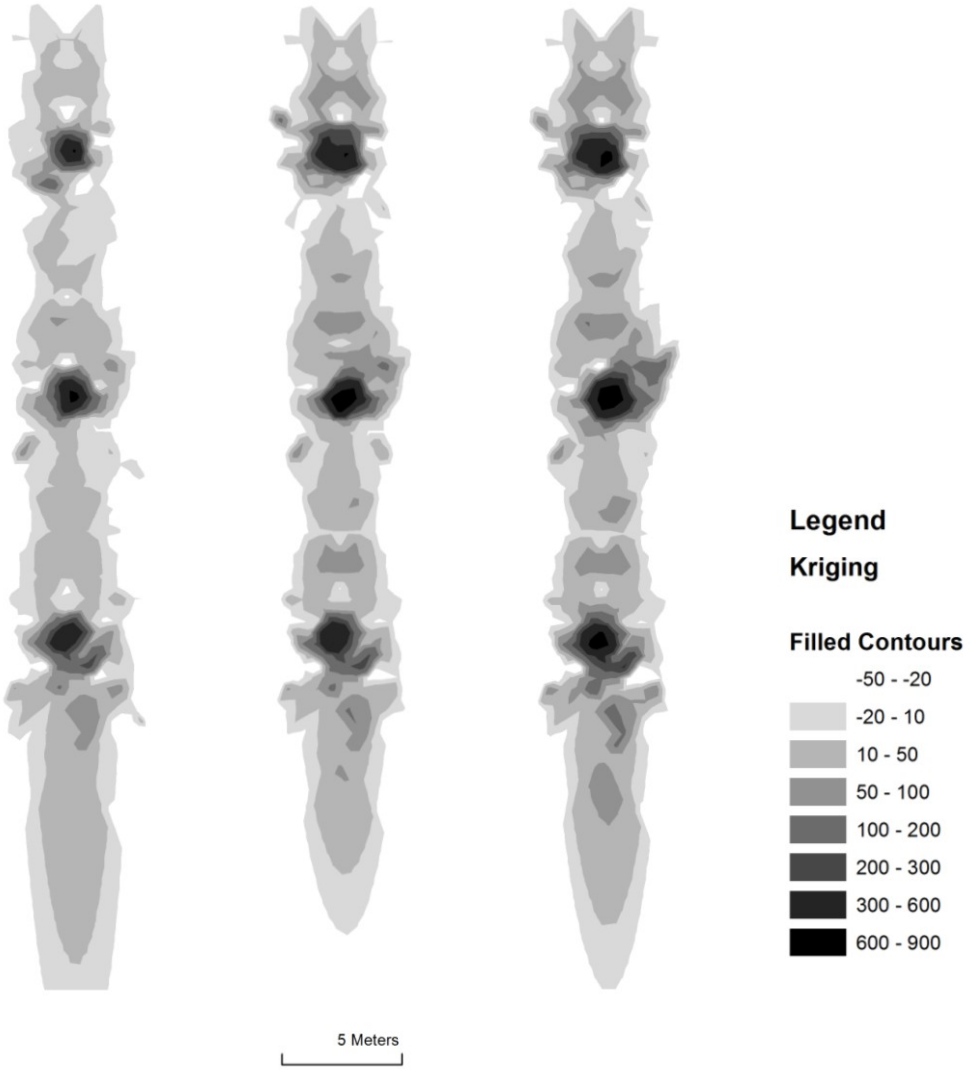

Figure 3.5. δD kriging map for 3 days of continued sampling (August 18th, 19th, and 20th). The darkness indicated the enrichment of δD value. From top to the bottom, they were plot 1, 2, and 3 in sequence.

From Figure 3.4, deuterium concentrations of one rhizome sample on the 4-m ring were still higher than the background indicating that water in the *A. donax* rhizomes can be transported at least that far.

In determining what fraction of water in the rhizomes was from simulated rainfall versus groundwater, δD of groundwater was set at an initial value δD_B (-26‰); after watering, δD_A was set to the means of each plot (1223‰, 1472‰, and 1415‰ for plot 1 to 3, respectively); and $\delta D_{Rhizome}$ was set to individual rhizome values (179 ~ 886‰). Water uptake for individual ramets based on the mass balance mixing model predicted that 35% (range from 14% to 61%) of water came from simulated rainfall and the others was taken from groundwater or deeper soil water. Furthermore, I assumed the two water sources for the rhizomes located at 4-m ring were groundwater and the rhizome located at 0.5-m ring. Again using the mass balance mixing model, it predicted that 9% of water in the rhizomes of 4-m ring came from 0.5-m rhizomes.

DISCUSSION

Consistent with my initial hypotheses, the change in ramet morphology after rhizome severing and evidence of deuterium water transport suggest that *Arundo donax* can share resources through interconnected rhizomes. Because of clonal integration, *A. donax* grew bigger and taller ramets after 11 weeks. Surprisingly, without the support from neighboring ramets, *A. donax* produced denser ramets initially but suffered higher ramet mortality during flooding.

Rhizome Severing Experiment

Initially, there was a rapid increase in ramet resprouting after rhizome severing. This indicated that the loss of rhizome connection might actually stimulate a shoot propagation response. This phenomenon is commonly observed in a variety of clonal plants, such as *Ammophila breviligulata* (Maun 1984)*, Scirpus canadensis* (Schmid and Bazzaz 1987), *Agropyron repens* (Maun 1984), and *Scirpus maritimus* (Charpentier et al. 1998). This also consistent with Guthrie's finding that cutting can increase *A. donax*'s density (Guthrie 2007). The increased ramet propagation due to rhizome severing has been attributed to loss of apical dominance within the clone (Schmid and Bazzaz 1987, Cline 1996, Hay and Newton 1996, Turnbull et al. 1997, Charpentier et al. 1998). The apical dominance, primarily controlled by auxin (Taylor et al. 1995), not only existed in individual shoots, but has also been shown to extend over a whole clone of connected ramets (Schmid and Bazzaz 1987). Thus, separation of rhizome connection can block the auxin transport and release of axillary buds from dormancy; then produce new ramets. On the other hand, bud inhibition can be caused by competition within the rhizome tissue for water, carbohydrate and nutrients (Nigam and McIntyre 1977). Therefore, the severance of rhizome connections could release ramets from competition.

Although rhizome severing initially enhanced the propagation of the ramets, it was also associated with higher mortality. The mortality of ramets could be due to the isolation of physiological integration only, or due to the combined effect of environmental stress (flooding) and rhizome severing. Prior evidence indicated that rhizome severing decreases survival of mature ramets of *Calamagrostis epigejos*

(Brezina et al. 2006). Plants decreased their productivity during and after the flood (refer to Chapter II) with limited oxygen supply to roots. For example, flooding has been shown to limit growth of *Phragmites* in a low marsh (Amsberry et al. 2000). Also, growth and clonal propagation has been shown to decrease with inundation depth (Xiao et al. 2011). Although plant performance decreased during the flood regardless of whether rhizomes were connected or not, physiological integration may increase the survival of the ramets under environmental stress. For instance, clonal integration enhanced the flood tolerance of *Spartina alterniflora* daughter ramets (Xiao et al. 2010). In this study, clonal integration played more important roles in severe flooding stress conditions and at early growth stages. With regards to *A. donax*, after about 8 days of flooding, plants were negatively affected by the inundated condition. However, given the fact that mortality of ramets with intact rhizomes was lower, clonal integration appears to increase ramet survival, probably by continually supplying nutrients and carbohydrates from neighboring ramets. Therefore, clonal integration is likely to increase the flood tolerance of *A. donax*.

The clonal integration in *Arundo donax* didn't increase the number of ramets produced, but did increase the growth of individual ramets. Maintaining physiological integration in *A. donax* appears to allow ramets to receive some resource from neighboring ramets. Individual ramets grew bigger and taller because they were able to exploit more resources than their roots can reach. This result was consistent with my initial hypothesis and is supported by experiments conducted on other species. A similar pattern was found in *Scirpus maritimus*, for which fewer ramets with bigger size were

observed in intact clones, as compared to more smaller ramets in isolated clones (Charpentier et al. 1998). Also, *Diphasiastrum digitatum* with severed rhizomes grew less vigorously (Railing and McCarthy 2000). Although the growth rate of *A. donax* increased in the individual ramet with intact rhizomes, I did not see measurable differences in plot-scale biomass after 11 weeks. This result was consistent with studies of *Schoenoplectus acutus* (Pauliukonis and Gough 2004), *Ammophila breviligulata* (Maun 1984), and *Scirpus maritimus* (Charpentier et al. 1998), in which final clone-level biomass and ramet production were the same regardless of whether rhizomes were intact or severed, although severing initially stimulated ramet production (Pauliukonis and Gough 2004). Due to the duration of experiment and flood disturbance, I didn't observe any difference in plot-level biomass between treatments; however, intact clones might have higher biomass over longer time periods because their ramets were more robust.

Plants might respond to disturbance and environmental conditions by altering plant morphology (Sutherland 1990). The morphological plasticity of clonal growth may also contribute to an invader's ability to spread rapidly in riparian zones (Maurer and Zedler 2002, Jakobs et al. 2004). Over the course of my 11-week experiment, the number of stems and size of plants suggests they responded to clonal damage as well as to resource availability by altering morphology. Nevertheless, *Arundo donax* was able to quickly produce new ramets and biomass from severed rhizomes, indicating that the survival and growth of this invasive species does not fully depend on resource sharing by the neighbor ramets. In other words, local resources taken up by individual ramets or small ramet groups were enough to allow *A. donax* to establish and grow in riparian

zones. In *Arundo donax*, similar to other clonal plants, the network of integration between ramets can be broken where disturbance (trampling or herbivory) occurs, in particular events that may occur during flooding (Bell 1997). Therefore, this invasive species can probably establish in a new habitat solely by taking up resources locally. Nevertheless, morphological plasticity and clonal integration can further enhance a rapid growth rate, increase its competitive capacity, and strengthen its ability to colonize disturbed areas and then maintain high growth rates after establishment.

Deuterium Labeling Experiment

Not only was clonal integration possible in *A. donax*, I also found that deuterium enriched water signal was transported from source to sink through rhizome pathways, probably beyond the range of root access. This conclusion is consistent with findings from other clonal species. De Kroon et al. (1996) suggested that in the heterogeneous condition, *Carex* rhizomes transport 30-60% of water from resource-abundant ramets to resource-poor ramets by clonal integration. Our regression model predicts resource sharing to distances of 2.17 m from the center (or 1.67 m from the edge) of the watering zone. I observed that about 9% of water transported from the watering area to the 4-m ring, which suggests that a small portion of total water uptake is shared long distances between connected ramets. Although I observed the labeled water signal beyond the watering range, of the possibility remains that labeled water was taken up by the lateral roots instead of shared through interconnected rhizomes.

Since we observed one sample where labeled water had traveled to the 4-m ring, there is also a possibility that water can be transported much further. With only 5

samples per ring, we might have missed the deuterium-enriched rhizomes when sampling at greater distances from the watering area, from 0.5 m to 4 m radius circle, because samples were spaced farther apart. Rhizome networks in clonal species with such long-lived rhizome systems are especially complex because of rhizome branching (De Kroon et al. 1991). As distances from the watering area increased, the likelihood of picking up the rhizomes with enriched signal decreased. Thus, only one sample was found that had enriched signal. Also, from the groundwater dilution perspective, farther away from the watering area, plants may have gradually relied more on groundwater because of diminished surface water uptake and water transport from neighboring ramets. For instance, if rhizomes are able to take up the water from their roots, they may not need to depend on clonal integration. Therefore, it could have highly diluted the enriched signal at greater distances from the watering area. Taking into account groundwater dilution, sampling points, and rhizomes network, it is very possible that maximum water transport can exceed the distances we observed in our experiment. Moreover, 14%-61% of labeled water was taken up by rhizomes after 3 days of watering, which implies that *A. donax* relied on both water sources. If the upper layer soil moisture was insufficient to maintain turgor, rhizomes may rely on groundwater. Since *A. donax* has huge rhizomes and deep enough roots to reach ground water, sharing of water and nutrients between ramets is probably only necessary when resource become limited. This is consistent with finding in Decruyenaere and Holt's research that precipitation has minor influence on seasonality and amount of recruitment of *A. donax* (Decruyenaere and Holt 2005).

In conclusion, I examined two important aspects of clonality in *Arundo donax*: the presence of physiological integration and the effects of physiological integrations among of connected ramets. The vascular connection of *Arundo donax* exhibited physiological integration, allowing them to grow more vigorously and better survive extreme conditions (flood and drought). Given the size of the rhizomes observed at our field sites, it is likely that clonal integration persists for many years; even if the aboveground parts of ramets become standing dead material (De Kroon et al. 1991). These factors may enhance competitive abilities of *A. donax* and other riparian invaders on the floodplain (Quinn et al. 2007). Furthermore, rhizome integration may also enhance the capability of ramets to exploit resources from areas with greater resource availability. This significantly benefits the plants living in resource-patchy riparian areas and might help it colonize less favorable habitats it could not have otherwise invaded.

CHAPTER IV

CONCLUSIONS

Performance of *Arundo donax* responded to water availability at both short-term and long-term scales. At short-term scales, *A. donax* adversely responded to both drought and inundated conditions, which has been observed in both observational and experimental studies. Over longer time scales, well-established populations of *A. donax* can tolerate a wide range of moisture conditions and maintain a high level of performance via improving its water use efficiency (Christou et al. 2003) and possibility of switching water sources, which eventually exhibits a relatively uniform growth in riparian zones.

Geomorphology controlled all of the gradients observed in this study. Increasing elevation was associated with decreasing surface soil moisture but low flood frequency and short inundated condition. River hydraulic sorting resulted in a strong soil texture gradient, which affected both soil moisture and nitrogen content. Thus, soil texture tends to counteract the effects of distance from river and relative elevation, which enhanced the uniformity of vegetation performance to some extent across the floodplain.

Arundo donax not only takes up the water locally, but also transports the water through its interconnected rhizomes. About 9% of resource taken up by resource-abundant ramets were transported to the resource-poor neighboring ramets 3.5 m away (at 4-m ring), while the median distance that the signal travelled was about 30 cm. Due to resource sharing from neighboring ramets, *A. donax* grows vigorously with robust

ramets and higher flood tolerance, which significantly benefits the plants living in the resource-patchy riparian areas and might help it colonize less favorable habitats it could not have otherwise invaded.

Clonal plasticity was observed in *Arundo donax* in response to rhizome severing and environmental gradients by altering plant morphology (Sutherland 1990). Under water-limited conditions, although stems were shorter, more structural material was produced aboveground, which minimized the plant energy cost and extended plant longevity. Rhizome severing stimulated 97% denser ramets initially, while intact rhizomes produced taller and bigger stems with higher flood tolerance over longer periods. Regardless, plot-level biomass was similar among plots with severed and intact rhizomes. This morphological plasticity of clonal growth may contribute to an invader's ability to spread rapidly in riparian zones (Maurer and Zedler 2002, Jakobs et al. 2004).

Nevertheless, *Arundo donax* performs relatively uniformly across riparian zones regardless of strong moisture gradients. I found that riparian geomorphology controls the environmental gradients which counteract each other and ultimately resulted in a resource-abundant environment. Intrinsically, clonal plant plasticity, regulating water use efficiency, and clonal integration ameliorate impacts of water stress on plant growth and performance. Therefore, both internal adjustment and external counteracting factors enhance its capability of establishment in a new habitat and then maintain high growth rates.

From the management perspective, the possibility of long-term eradication of *A. donax* from the Rio Grande may depend on an understanding of both intrinsic attributes

of this species and how it interacts with environmental factors in the riparian zones. My study was an important step toward such improved understanding. Although I assume *A. donax* can rely on both groundwater and surface water, we don't know which water source is more important for plants, which can be varied in response to age, rooting depth, and water availability. Understanding the amount of groundwater consumed by *A. donax* may give us insights on the invasion management in terms of water conservation. Secondly, we found that plants were negatively affected by flooding. However, these responses were only exhibited in the short-term and intermediate-term scales. More research should explore how flood duration affects the performance of this species over longer time scales. Third, I observed that the depth to groundwater table did not exceed 6 m within existing patches of *A. donax* I studied. Thus, there might be a point where groundwater is below the range of rooting depth and surface soil moisture in the upper layer becomes the main limiting factor. Beyond this point, *A. donax* may not be able to extend any further as drought conditions would occur too frequently.

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